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ARCHEOLOGY.—*Additional information on the Indian pottery from Pissaseck (Leedstown), Westmoreland County, Virginia.*[1] CARL F. MILLER, Bureau of American Ethnology.

After the death of David I. Bushnell, Jr., in 1941, a number of sherds marked "From Leedstown, 1936" were found among his possessions. These turned over to the Smithsonian Institution. It is assumed that the sherds, U. S. N. M. nos. 392206–7, were collected from the surface of a village site in or near Leedstown, Westmoreland County, Va.

Previously, Bushnell (1937) published on 12 sites below the falls of the Rappahannock River in Virginia, one of which is of special interest in that it deals with the material on hand—this is the village of Pissaseck upon which a portion of Leedstown was later built. Inasmuch as his pottery description of this site is rather meager, the collection warranted further study in order to point out the correlation with surrounding types of the same chronological age.

Pissaseck, as the village site was known during early colonial times, was a large aboriginal settlement. It stood on the north bank of the Rappahannock River and was represented by Capt. John Smith (1884) on his map of 1624 with a "Kings Howse" to show its relative importance. This village was not mentioned in the earlier narratives of 1608 when Smith and his party went up the river. Smith's map of 1624 indicated a number of villages occupying position along the Rappahannock River which were no longer evident when Hermann (SEE: Bushnell, 1937, p. 11) mapped the same area in 1673. Thus, just a little over 50 years after Captain Smith had been conducted by his Indian captors to their settlements on the banks of the Rappahannock, the native population of the entire valley had been dispersed and many of their village sites had become the property of English settlers.

Using Tooker (1911), a self-styled Algonkinist, as a source of information, an attempt was made to determine the meaning of the word "Pissaseck." It was found that the suffix "seck" is mostly spelled "suck," which has been interpreted to mean "brook," "creek," "outlet," or "a small stream flowing out of a pond." The stem of the word, "piss," was interpreted to mean either a "mire," "meadow," or "marsh." Knowing that the village was located on a level area above the river, below and adjoining an extensive marsh, known as Drakes (Drake's) Marsh, presents a clue as to the possible suggested meaning of the word. From the above study, the possible suggested meaning may be: *the place where the marsh empties into the river.*

Smith noted that Pissaseck occupied a level area above the river, below and adjoining an extensive marsh, known as Drakes Marsh, where there was much game and wildfowl to be found. Vast amounts of broken pottery and innumerable objects of stone covered the surface of this area. The description conforms to one made by Strachey (1849). He tells us that:

> Their habitations or townes are for the most part by the rivers, or not far distant from fresh springs, commonly upon a rive of a hill, that they may overlooke the river, and take every small thing into view which sturrs upon the same. Their howses are not many in one towne, and those that are stand dissite (dispersed) and scattered without forme of a street, far and wyde assunder.

[1] Published by permission of the Secretary, Smithsonian Institution.

In going over the early records of this section of Virginia, we find allusions to the Iroquois bringing pressure to bear upon the small loosely grouped Algonquian towns causing them to move into more concentrated areas for mutual protection. The intrusion of white man's settlements hastened this regrouping and later final abandonment. The Iroquois were pushing them around in 1608 and by 1624 the village was well established only to be abandoned some time before 1673.

The area of the falls of the Rappahannock River formed "the bounds betwixt the Kingdome of the *Mannahocks* and the *Nandtaughtacunds*." Apparently the *Mannahocks* were the better known *Manahoac* tribes which have been assigned to the *Siouan* group, while the *Nandtaughtacunds* formed a part of the *Powhatan Confederacy* which were of *Algonquian* stock. The territory occupied and claimed by the Algonquian group in Virginia included the tidewater section from the Potomac south to the divide between Jamestown Island and Albemarle Sound, N. C., and extended into the interior as far as the falls of the principal rivers about Fredericksburg and Richmond. To the west of them in the Piedmont region were the hostile *Monacan* and *Manahoac*, while to the south were the *Chowanoc*, *Nottoway*, and *Meherrin* of Iroquoian stock. It seems that no considerable number of the Powhatan Indians ever removed from the general tidewater area of the Chesapeake Bay. Apparently they just gradually died out or retired into one or two small reservations where a number of mixed-bloods still live.

Bushnell (1937) indicated that by the latter part of the seventeenth century the English traders were probably well established in the town of "Leeds" at or near the Indian village of Pissaseck. It was during the meeting of the General Assembly that convened at Williamsburg, Va., in May 1742 that an Act was passed for the establishment of a town "on the north side of the Rappahannock River in the County of King George, where the church and public warehouses are built . . . The said town shall be called by the name of Leeds."

Later Leeds became known as Leedstown. It was an active center of trade, with wharves and warehouses from which vast quantities of tobacco and other products of the colony were sent to England and where sailing vessels landed supplies for the rich plantations on the Northern Neck.

> Scant traces of the colonial town remain, and these are now encountered intermingled with the stone implements and bits of earthen vessels made and used by the earlier occupants of the region. However, the brick structures erected in the town covered only part of the land that had formerly been included in the native settlements, assuming the site to have been occupied and reoccupied through generations, long before the coming of the English. (Bushnell, 1937, p. 18.)

ARCHEOLOGY

Holmes (1903), in his study of Algonquian pottery, thought that this pottery was developed mainly in the general region from a common source and was manufactured by all members of the Powhatan Confederacy as well as other members of the same stock along the Carolina coast. He suggested that environment may have played a large part in the rate of its development resulting in a tendency of keeping it rather simple in form and uniform throughout the whole Algonquian cultural area. Why a group who was relatively skillful in other arts, such as the cultivation of maize, etc., should keep their pottery-making in such a simple form is rather hard to explain. By "simple form" we mean that all vessel types were confined to deep bowls and wide mouthed pots of medium to small size. Holmes (1903) further states:

> Save in remote sections where western and southern tribes are known to have wandered, we do not encounter such features as eccentric or compound forms, animal shapes, constricted mouths, high necks, handles, legs, or flat bases of any kind. Ornament is archaic, and curved lines are almost unknown. These statements are in the main true of the whole Atlantic Algonquian belt from Albemarle Sound to the Bay of Fundy.

Even though the ware was simple in form and decorated with archaic-looking methods it was well made and shaped. Supposedly the vessels are largely if not exclusively culinary in nature.

A fair number of sherds demonstrates that the ware was manufactured by means of

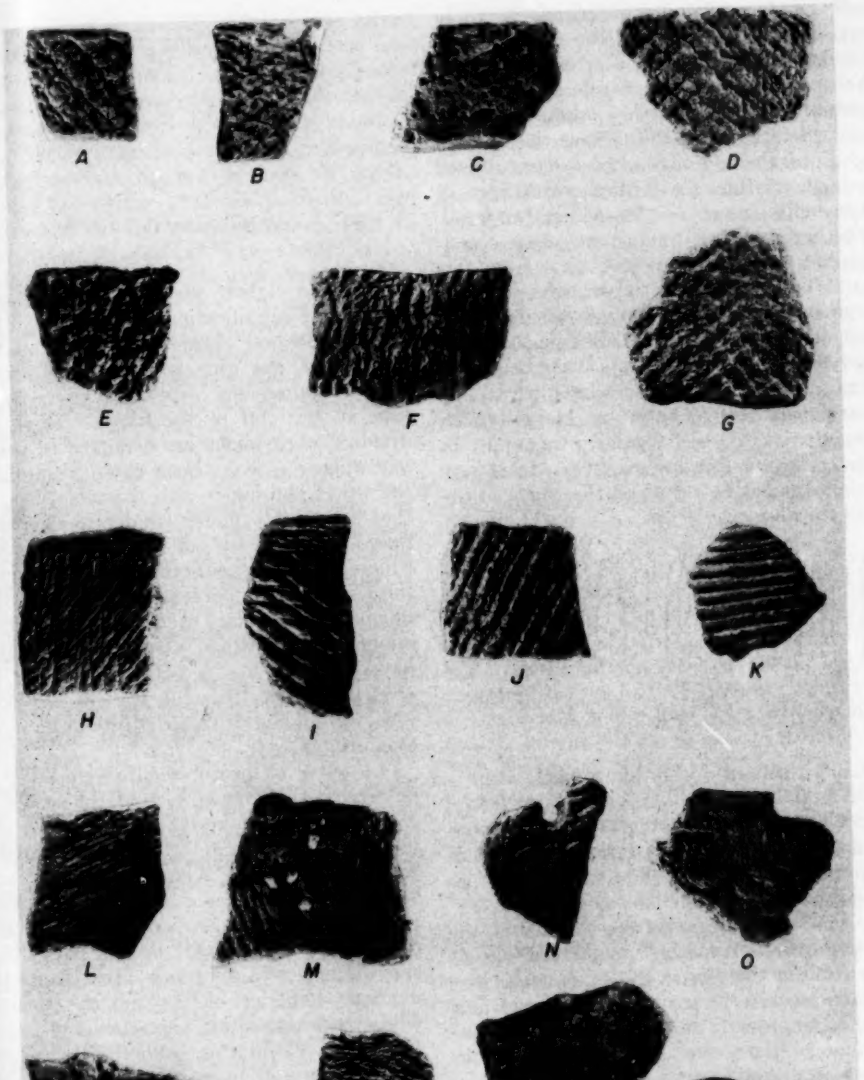

FIG. 1.—Sherd types from Pissaseck (Leedstown), Va.: Net-impressed A–E; Fabric-impressed F, G, O, and Q; Cord-wrapped paddled H–N; Plain P, R′, and R″.

coiling and that a uniform thickness throughout the vessel is not the usual result. Thickness varies from place to place within the same body wall. As a rule the bases are medium thin with the adjoining walls thickest tapering in thinness as the lip area is approached. Local clays were utilized throughout the area with a wide range of ingredients used as tempering material. Whether type of temper has any stratigraphic significance is not known at this time. Tempering material consists of sand, large particles of grit, pulverized limestone and just a trace of crushed shell. Sand particles vary in size from very fine, less than 1.0 mm in diameter, to comparatively coarse particles of grit or gravel which ranged from 4.0 to 5.0 mm in diameter. In some cases the grit and gravel particles were so large that they occupied the whole of the wall thickness.

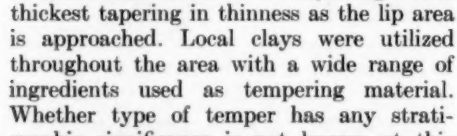

FIG. 2.—LIP FORMS: Cord-wrapped paddle—sand tempered. *f* had faint cord impression on the lip area.

Color, caused by firing, ranges from a light buff into a reddish brown and into a chocolate-gray, indicating either a reduced or an oxidized condition during this stage of manufacture. Evidences of fire clouds are found on the exterior of sherds.

As far as we can tell from the sherds, the surfaces were smoothed while the vessels were still in the plastic state. After this any subsequent exterior treatment was performed, such as impressing fabrics or textiles into the surface of the vessel so as to decorate or ameliorate it.

Lips, in all instances, are simple being either rounded or flattened with gradations between the two showing on a single specimen. One sherd has a scalloped edge formed by pressing a medium heavy cord into the soft walls of the vessel at intervals roughly about an inch apart. Such treatment is the exception rather than the rule and is not characteristic of the whole assemblage.

FIG. 3.—Principal vessel shape as restored from sherds.

Rims are slightly modified for the esthetic effect. One modification that occurs in the fabric-impressed ware was found on the interior of the rim where a number of trough impressions were arranged side by side at the top of the vessel. These individual impressions are arranged in a row and appear to have been made by pushing the tip of the finger into the moist clay so that a line of semicircular depressions were raised on the side of the vessel toward which the force was applied. Other samples show further modification in that this pinched effect has been smoothed down eradicating the ripple effect leaving a slight bevel instead. As a consequence the lip area is thinner than the wall of the neck area. No folding or collar effects in the neck area are present.

A number of measurements were taken to determine the over-all size of the orifice of various vessels represented within the collection. It was found that they averaged around 9 inches (22.7 cm) in diameter with some smaller and some larger. In this same manner, the average body diameter and depth were determined. It was found that the diameter varied very little from the average diameter of the mouth opening, while the mean depth was around 11 inches (28.0 cm). Estimating from these measurements we would judge the volumetric content of an average vessel to be around 2 gallons, with some of the smaller ones holding around 2 quarts.

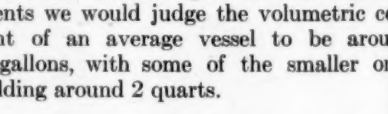

FIG. 4.—LIP FORMS: Plain ware, *a*—shell tempered; *b*—limestone tempered; *c*—*h* sand tempered.

We find that the Algonquian was given to the use of cordage and textile fabric impression as a means of embellishing his vessels—either intentional or accidental. Generally, the entire body of the vessel is covered with impressions of either coarse cloths, various texture of nets or cords. Besides the textile impressions there a few cases in which punctations occur, Fig. 1, R′. These punctations are rather large, diameter 6 mm, which almost pierce the exterior walls of the vessel leaving a node or pustule opposite each separate punctation on the interior of the vessel, Fig. 1, R′ and R″. Similar punctations have been reported for other sections of the eastern seaboard.

SUMMARY AND CONCLUSIONS

As near as we could determine, the pottery recovered from Pissaseck was manufactured by means of coiling and some molding out of local clays. A number of fractures along the original coils clearly demonstrate the method of manufacture. This was further demonstrated when small fragments or sections were broken off each sherd to test for tempering. In a number of cases these breaks occurred at the juncture of the two coils. The pottery was developed mainly in the general region from some unknown origin and was made by all members of the Powhatan Confederacy and to some extent by outside groups coming under their influence.

FIG. 5.—LIP FORMS: Net-impressed wares; all are sand tempered. "*i*" shows scalloped edge. Slight cord impressions occurred on: *a*, *d*, and *h*.

In testing for temper each individual sherd was freshly broken in order to examine an unweathered rather than a long exposed surface. Four different types of tempering materials were identified: sand, crushed quartz, crushed limestone and crushed shell with but small emphasis on particles of water worn gravel. The majority of the sherds were tempered with either sand or crushed quartz (grit), next to be followed by crushed limestone while crushed shell was just barely represented. Of the latter two, most of the tempering material had leached away leaving only the impressions of the original material and as a consequence all sherds thus effected were filled with a number of holes. This feature makes the sherd fragments comparatively light in weight. Sand particles are usually small with rounded edges. The actual amount of sand used readily determines that the roughness of the paste is in direct ratio to the amount of sand used as tempering material. Crushed quartz, or grit, varies in diameter from 1 to 5 mm. In the latter case some particles of the larger size have been noted to occupy the complete thickness of the body wall of the vessel and can readily be recognized on the interior as well as the exterior wall. This characteristic is demonstrated in Fig. 1, M.

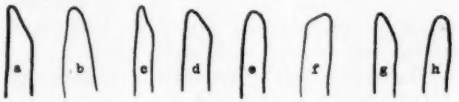

FIG. 6.—LIP FORMS: Fabric-impressed ware. *a*, *c*, and *g* have been modified by pinching. Slight nodes are present on the interior surface formed by pinching on *a*. *c* and *g* have been smoothed. Interior surfaces are represented to the right on each profile.

Again, we say that the color ranges from a light buff through light orange through grays and in one instance is a real dark gray or black.

As a rule, after the vessel was fashioned, the surfaces were roughly smoothed. In the decorated wares and various impressions were next applied to the exterior only and the vessel allowed to dry before firing. While the vessel was still plastic any other alterations such as finger pinching on the interior rim of the vessel, beveling of the rim area in the interior of the vessel, as well as giving the rim a scalloped effect was then performed.

Decoration, if truly it was thus, consists of the impressing of various sized nets, fabrics, cords, and baskets on the exterior of the vessel. In addition, a cord-wrapped paddle was used to apply the impressions of parallel arranged sections of cords to the exterior.

Bushnell (1937) tells about one sherd which was found at Pissaseck "decorated with straight, very regular lines, which had been made by impressing some hard material into the clay when the latter was in a plastic state." This technique has been termed "simple stamping" and is illustrated in his plate 7, *a*. It appears that this sherd was tempered, at one time, with crushed limestone which had leached away leaving a surface similar to Fig. 1, P.

Funkhouser and Webb (1929, pp. 86–102) noted five different types of materials utilized to impart this simple stamping technique to exteriors of vessels. These are: shredded fibrous bark, stems and leaves of some of the tough wiry grass, flat strips of bark, flat pieces of corn husk or stalk, and narrow strips of skin or leather. They listed additional material thus used which include: pawpaw, Indian hemp, milkweed, cat tail, rushes, and inner bark of leatherwood or moosewood, linden or basswood, rattlesnake master and canary grass.

Bushnell (1937) illustrates a number of textile types identified from pottery fragments from Nandtanghtacund which are almost identical to those recognized on the sherds from Pissaseck. Comparable surface treatment is to be found through the Algonquian area with slight modification noted in borderline areas.

Rims are usually straight with only an occasional one showing a slight incurving of the exterior wall. Rims are usually of the same thickness as the body wall; in only three instances are they thinner than the wall. A distinct rim modification appears in the form of medium large punctations which form nodes or pustules within the throat section of the vessel.

Lips, as a rule, are very simple either rounded, flattened and sometimes beveled. Only rarely has the impression of cords carried over onto this area of the vessel. Of all the lips in the collection only one has been fashioned into a scalloplike appearance. This was brought about by impressing into the plastic clay a cord whose impression is to be found in the troughs of the scallop.

The typical body form is cylindrical and tapering down to a rounded base. The body is not of uniform thickness, as thickened portions appear throughout the vessel. Bases are no thicker than the average wall.

All specimens in the present collection, after they were separated into the various decorative types, were measured for thickness. Plain sherds, which may have originally formed the basal portions of decorated vessels, ranged from 3 to 13 mm, with a mean of 8 mm; net-impressed ranged from 5 to 11 mm with a mean of 7.5 mm; cord-wrapped paddle, taken as a whole irrespective of the diameter of the elements, ranged from 4 to 12 mm with an average of 8 mm; fabric-impressed ranged from 5 to 12 mm with an average of 8.5 mm.

The type of pottery found here is characteristic of the Algonquian groups found north to the Bay of Fundy, between Nova Scotia and New Brunswick, Canada, and south to Albemarle Sound in North Carolina. The southern portion extended westward to the falls of the principal rivers around Clarksville, Fredericksburg, and Richmond, Va. This wide range will allow for a number of local variants. It is believed that the pottery types found along the Rappahannock belong to this general classification. It is also felt that certain influences coming in from the Ohio Valley may have influenced it to some extent.

On one plain sherd there is the appearance of the use of a red slip both interiorly and exteriorly. Under magnification it appears as a thin light red layer 0.25 mm in thickness with no penetration into the core of the sherd. The slip is much thicker on the exterior than it is on the interior and appears as though it was brushed on lightly over this surface. The sherd is tempered with moderate sized grains of sand. The slip has been rubbed somewhat, but was not polished.

There is no direct evidence of the use of handles or lugs of any description on the pottery from this area. Bushnell (1937) illustrates a handle in his plate 7, *b*, which could have been an importation from farther west since such features are customarily found along the headwaters of the James.

It would appear that the ceramic trend of the sites along the Rappahannock River was toward a transition from purely early Woodland into an early aspect of Algonquian tradition which may be termed a late phase

of late Woodland. This is paralleled in the tempering material which is sand and grit in the early stages and crushed limestone and shell in the later ones. Up to this stage there is no complexity in vessel shapes and form, and such embellishments as lugs, handles and feet are lacking.

TECHNOLOGICAL AND ARTISTIC ACTIVITY

POTTERY COMPLEX:

- Manufactured by means of the coiling system
- Manufactured by molding, rare
- Tempered with:
  - Sand
  - Crushed quartz (Figure M)
  - Crushed limestone (Figure P)
  - Crushed shell, rare
- Deep bowl shapes dominant
- Wide-mouthed jars, present
- No handles, lugs or feet
- Lips are simple
- Rims are straight
- Rims occasionally partially punctuated with nodes or pustules on the interior, throat area, of vessels (Fig. 1, R′, R″)
- Drill holes below lips (Fig. 1, N)
- Net-impressed (Fig. 1, A, B, C, D, N)
- Fabric-impressed (Fig. 1, G, O. Q)
- Cord-wrapped paddle impressed (Fig. 1, H, I, J, K, L, M)
- Plain smoothed (Fig. 1, P, R″)
- Basket impressed (Fig. 1, F)

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PALEONTOLOGY.—*The morphology and classification of the oldhaminid brachiopods.* ALWYN WILLIAMS,[1] Glasgow University. (Communicated by G. Arthur Cooper.)

The grotesque nature of that short-lived but widespread group of brachiopods including *Oldhamina* Waagen and *Leptodus*[2] has long been a source of palaeontological interest and has led to many conflicting interpretations of the morphology and habit. Before Waagen's masterly exposition (1887) of the morphology and affinities of the group the occasional specimen obtained from the marine Permian of China and India were so confusing that de Koninck described *Oldhamina* as a bellerophon and Kayser named *Leptodus* in the belief that it represented part of a fish skeleton.

In the past 50 years a number of important papers, notably by Fredericks (1925), Watson (1917), Wanner (1935), and Licharew (1932), have not only substantiated Waagen's conclusions but also added greatly to our knowledge of the diversification and derivation of the group so that now there is no doubt that although the oldhaminids are exceptional in a number of characteristics they were derived from the normal strophomenoids and are but unusual members of that group.

Oldhaminid peculiarities are manifold. The shell is disproportionately inequivalve, the hinge-line together with the articulatory apparatus is rudimentary and the muscles (as judged from the muscle scars) were correspondingly degenerate and often asymmetrically developed, the brachial valve

[1] I record with pleasure the stimulating and helpful discussions I have had with Prof. T. N. George and Mr. G. Owen, both of Glasgow University, on the subject matter of this paper.

[2] The use of *Lyttonia* Waagen, 1887, in place of *Leptodus* Kayser, 1883, is without warrant.

is typically highly lobate and the pedicle valve equipped with a complementary septal apparatus. But unusual as these features are the shell structure of the brachial valve appears to be the most radical departure from that of normal brachiopods.

SHELL FORM AND STRUCTURE

In all articulate brachiopods the shell, excluding the periostracum, is composed of two layers, an outer lamellar layer of constant thickness consisting of a mosaic of calcitic platelets and an inner fibrous layer of variable thickness built up of fibrous calcite. Work on the relationship between the shell and mantle in modern *Terebratulina* to be published jointly with G. Owen in the near future has shown that the differentiation of the shell layers begins at the mantle edge (Pl. 1, Fig. 1). The lamellar layer is deposited only by a few epithelial cells forming the tip of the outer lobe, the deposition of the fibrous layer begins immediately behind this narrow lamellar zone and is carried on to a varying degree by the outer epithelial layer of the mantle over the entire shell surface. Thus all internal processes and protuberances such as the terebratuloid loop are composed only of fibrous calcite and are deposited by enveloping invaginations of the outer epithelial layer of the mantle.

The shell of the oldhaminid pedicle valve (Pl. 2, Figs. 6, 7) is like that of any other brachiopod. It consists of an outer lamellar layer, and an inner fibrous layer traversed as in all strophomenoids by spicules of cryptocrystalline calcite which do not penetrate the lamellar layer but protrude through the innermost fibrous layers to give the internal shell surface a tuberculate appearance.

The brachial valve (Pl. 2, Fig. 2) however appears not to possess this twofold differentiation of the shell, for the outer lamellar layer is almost completely absent, the entire shell anterior to a small apical triangular area being composed only of fibrous calcite so that the external and internal surfaces are pierced by spicules. The absence of the lamellar layer over so large an area is not known in any other brachiopod and calls for a reinterpretation of the nature and growth of the brachial valve.

If analogy with modern terebratuloids is valid and in strophomenoids, too, those structures which are composed only of fibrous material were deposited within invaginations of the outer epithelium, then that part of the oldhaminid brachial valve which is also composed of fibrous calcite was strictly internal and formed no part of the protective shell. In this event most of the structure hitherto identified as the brachial valve is no more than an internal skeletal support to a highly lobated mantle infold.

The brachial valve which in normal brachiopods is a part of the enclosing protective covering to the viscera and mantle is thus vestigial and obsolescent. It is represented by the small obtusely triangular portion of the shell situated apically and consisting of the usual outer lamellar layer and inner fibrous layers. It forms only the lobes of the degenerate cardinal process and the posterior part of the denticular sockets (Pl. 1, Figs. 3–5).

This interpretation is not as far-fetched as first impressions convey. Comparable developments in the strophomenoids are found in both the thecideids and the plectambonaceids whose strongly elevated platforms, deposited by the outer epithelium, are developed for the support of the lophophore. In the plectambonaceid *Leptelloidea musca* Öpik (cf. Figs. 6, 7 of Pl. 1) the lophophore platform is so pronounced that it protrudes well into the interior for over half the length of the shell as a bilobed pseudopunctate plate diverging from the brachial valve just anterior to the cardinalia. The difference between such a development and that of the oldhaminids lies in the disproportionate size of the oldhaminid internal plate in comparison with the brachial valve the growth of which was arrested at an early stage of development.

The extraordinary development of the oldhaminid brachial valve and internal plate possibly occurred in the following manner. During the earliest stages of growth both lamellar and fibrous layers were laid down by the mantle which advanced from an initial locus of growth lying immediately posterior to the cardinal process and expanded laterally to cover an obtusely triangular area. Such a structure is reminiscent of an obsolescent interarea and chilidium but hardly homologous with them for the direction of growth was the reverse of that governing the deposition of a true interarea and chilidium. The mantle edge did not advance beyond the base of the triangular lamellar layer; but as growth proceeded the outer epithelial layer continued the enlargement of the incipient cardinalia and an inwardly directed plate-like ridge, the latter

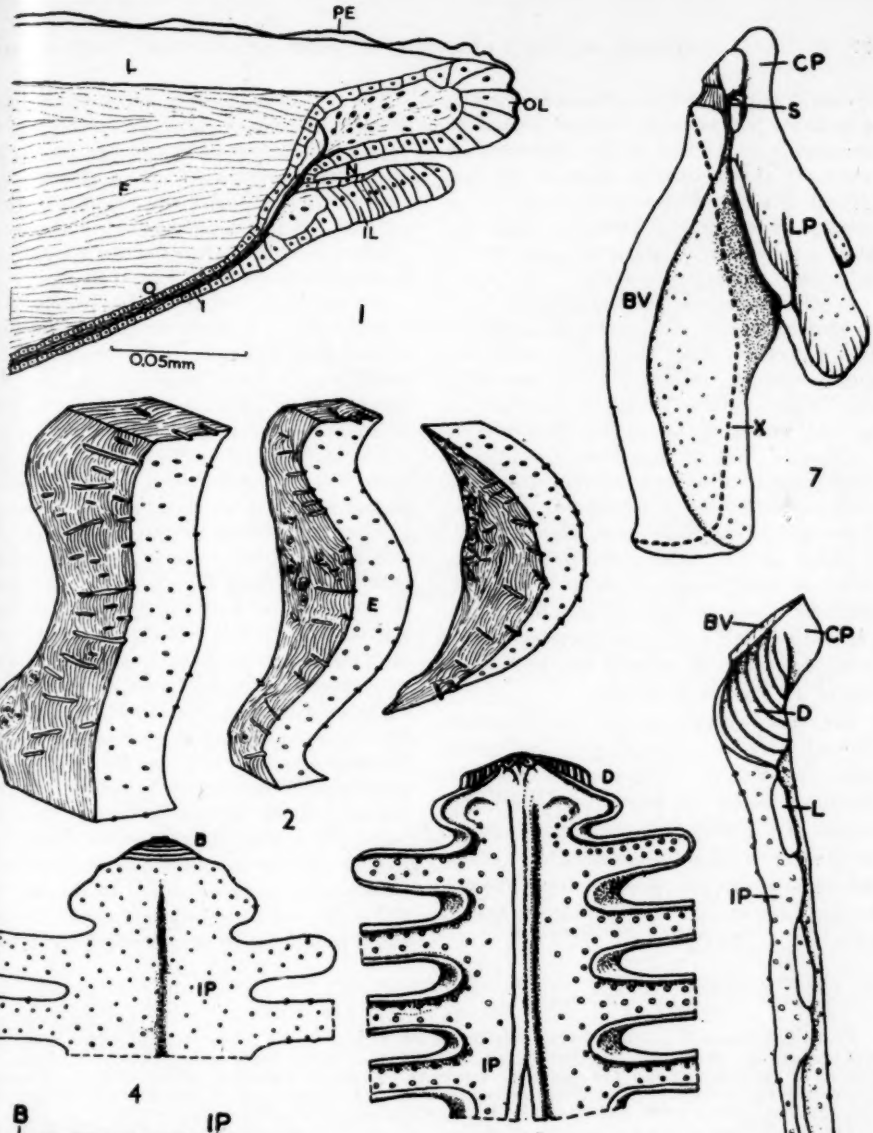

PLATE 1

FIG. 1.—Radial section through the mantle edge of *Terebratulina* sp., Crinan Loch, Scotland, showing the relationship between the shell and the mantle lobes: F, fibrous layer; I, inner epithelium; IL, inner lobe; L, lamellar layer; N, setal groove; PE, periostracum; O, outer epithelium; OL, outer lobe.

FIG. 2.—Structure of a lobe of the brachial internal plate of *Oldhamina decipiens* Koninck as reconstructed from serial sections of specimen BM. 18646, Permian, Salt Range, India: I, internal surface; E, external surface. (× 10)

FIGS. 3–5.—Internal, external, and lateral views respectively of the posterior portion of brachial valve and internal plate of *Leptodus* sp. Permian (Word), W. Texas: B, vestigial brachial valve; D, sockets for dental areas; IP, internal plate. (× 3)

FIG. 6.—Enlargement (× 6) of Fig. 5 for comparison with Fig. 7 representing a lateral view of *Leptelloidea musca* Opik, Middle Ordovician, Baltic Provinces (× 7): BV, brachial valve; CP, cardinal process; D, socket for dental areas; IP, internal plate; L, lobe; LP, lophophore platform; S, socket; X, external profile of brachial valve.

encased in an epithelial sac, expanding anteriorly to form the internal plate. General oldhaminid morphogeny would lead in the subsequent development of the internal plate to the early appearance of a median incision by the accelerated growth of the submedian areas, and later, in phylogeny as well as ontogeny, the appearance of the lateral lobes.

In addition to imparting rigidity to the infold of the dorsal mantle, the internal plate probably gave support to the lophophore, a conclusion already advocated especially by Watson (1917) and Wanner (1935). The most primitive oldhaminid known is the upper Pennsylvanian *Poikilosakos* Watson, immature specimens of which possess a subcircular internal plate with a median incision (cf. *Cardinocrania* Waagen). If the lophophore was adherent to the periphery of such a plate it closely resembled the schizolophus so characteristic of many brachiopods. Moreover if the lobation of the internal plate was accompanied by a corresponding lobation of the lophophore it assumed the familiar pattern of the ptycholophous stage.

The shell composition of the oldhaminid brachial valve then, suggests that the brachial valve proper is a vestigial apical triangular structure, whereas the greater part of the shell consists of a lobated plate ensheathed in mantle tissue and giving support during life to a schizolophous or ptycholophous lophophore. The oldhaminid brachiopods were therefore functionally univalves (Pl. 2, Fig. 8).

The oldhaminid pedicle valve was normally developed to form a protective covering to the viscera and the ventral mantle lobe by which it was deposited; although it must be noted that, since the brachial valve and associated internal plate lay well within the periphery of the pedicle valve, a considerable area of the mantle must have been exposed.

The structure of the posterior portion of the pedicle valve is however exceptional. The apex of the valve is usually malformed through attachment, but it is evident that in place of an interarea there existed a small triangular patch of lamellar calcite which lay immediately posterior to the vestigial brachial valve (Pl. 2, Figs. 3, 4). This triangular patch forms the posteromedian area of an enormous flap of fibrous and lamellar shell material apparently representing an extension of the posterior part of the pedicle valve and invariably sharply reflexed just dorsal of the base of the triangular lamellar layer. The shape of the flap varies considerably: specimens attached to a regular surface possess a flap which resembles a pair of expanded ears extending laterally from the median reflexed area (Pl. 2, Fig. 5); in those which lay free on the sea floor throughout most of their lives the flap is greatly extroverted so that the distal edge is usually in contact with the external surface of the pedicle valve (Pl. 2, Fig. 1); in those attached to irregular surfaces or crinoid stems the flap is closely adherent and moulded to the base (Pl. 2, Fig. 3); and in two distinct stocks, *Chaoella* and *Adriana*, the flap grew forward and is anky-

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PLATE 2

FIG. 1.—Submedian portion of the posterior flap of *Oldhamina decipiens*, reconstructed from serial sections of BM. 18646, Permian, Salt Range, India: 1, 2, 3, 4, and 5 are successive layers of shell deposited by the posterior flap, the circles (R) represent the minimum point of retractibility of the mantle flap necessary for the deposition of each succeeding layer; D, dental area; L, lamellar layer; P, pseudopunctate fibrous layer; PV, pedicle valve; T, triangular area of lamellar calcite. (× 9)

FIG. 2.—Submedian view of interior of pedicle valve of *Chaoella* sp., Permian (Leonard) W. Texas: L, lamellar layer; P, pseudopunctate fibrous layer; PF, posterior flap; PV, pedicle valve; T, triangular area of lamellar calcite. (× 2.5)

FIGS. 3, 4.—Submedian and posterior views of the apical part of the pedicle valve of *Leptodus* sp., Permian (Word), Texas: D, dental area; L, lamellar layer; P, pseudopunctate fibrous layer; PF, posterior flap; PV, pedicle valve; R, reflexed region of posterior flat; T, triangular area of lamellar calcite. (× 3)

FIG. 5.—Apical part of pedicle valve of *Leptodus* sp., Permian (Word) Texas: D, dental area; PF, posterior flap; PV, pedicle valve. (× 3)

FIGS. 6, 7.—Portion of septal apparatus of *Leptodus* cf. *richthofeni* Kayser, Permian (Sosio), Sicily and *Oldhamina decipiens*, Permian, Salt Range, India respectively, reconstructed from serial sections: L, lamellar layer; F, pseudopunctate fibrous layer. (× 8)

FIG. 8.—Submedian view of a reconstruction of a *Leptodus* to show the relationship between the mantle and the shell (portrayed in solid black in section): C, cirrus of schizolophous lophophore; EM, exposed part of the ventral mantle lobe (M); IP, internal plate enveloped by an infold of the dorsal mantle lobe; PF, retractible posterior flap; V, visceral region.

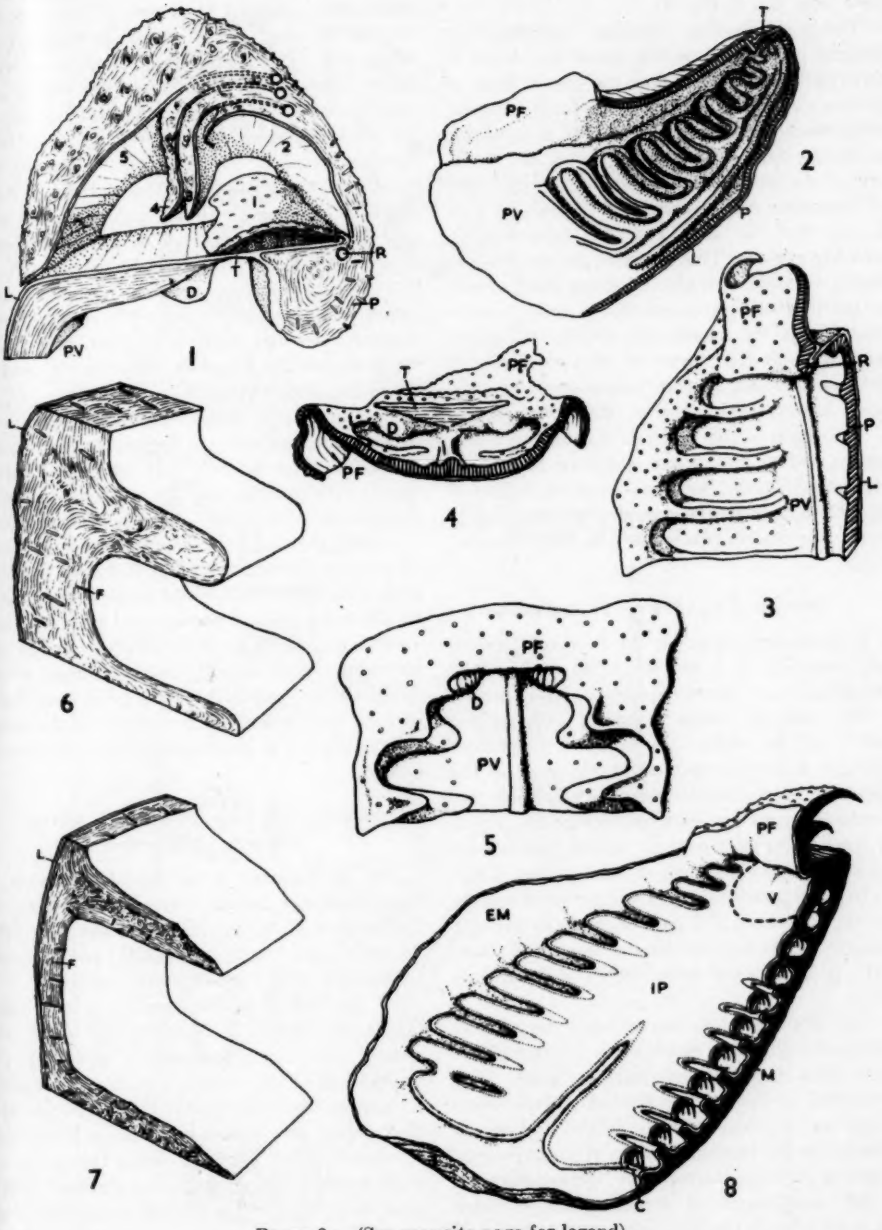

PLATE 2.— (See opposite page for legend).

losed to the sides of the pedicle valve to form a deep cone (Pl. 2, Fig. 2).

The posterior flap, although apparently an integral part of the pedicle valve, lies dorsal to the brachial valve and was the prime organ of fixation (indeed the only one in those oldhaminids attached to crinoid stems). It is envisaged as having been laid down by a posterior extension of the mantle capable of a rapid deposition of cementing shell material and disposed in such a way that the inner epithelial layer was invariably exposed. This posterior mantle flap was highly variable in shape, moulding itself closely to the base of attachment and it must be concluded that the mantle was greatly retractible so that paper-thin layers of shell consisting of both fibrous and lamellar calcite could be plastered one on top of another (Pl. 2, Fig. 1).

The origin of the posterior mantle flap is unknown, for no homologue is known to exist in other brachiopods; but it is a constant feature of all oldhaminids and is as prominent in primitive forms like *Poikilosakos* as it is in later Permian forms.

THE ARTICULATORY APPARATUS

If these conclusions on the form of the shell are acceptable it is not surprising to find that the leptodid articulatory apparatus is degenerate.

The cardinal process is undoubtedly bilobed but is usually rather inconspicuous in marked contrast to the pronounced development of the structure among strophomenoids generally. Anterolaterally to the cardinal process lie a pair of concave surfaces oval in outline and extending down to the first pair of lateral lobes. These surfaces are usually striated and represent sockets for the reception of a pair of similarly striated slightly convex surfaces (dental areas of Watson, 1917, p. 213) in the apical region of the pedicle valve.

The fact that the muscle scars are usually asymmetrically and sporadically impressed has been fully discussed by paleontologists. Well preserved interiors of the brachial valves sometimes bear a pair of variably defined impressions anterior to the cardinal process which have been taken to be the adductor scars. Occasionally too a full complement of diductor and adductor scars may be seen in the postero-median region of the interior of the pedicle valve (e.g., *Poikilosakos variabile* Wanner and Sieverts, 1935); and it seems that the diductors, when normally disposed, were inserted in a pair of narrowly divergent depressed areas sometimes bounded by ridges and lying lateral to submedian adductor scars. These scars however are frequently unequally developed and asymmetrically disposed. In *Poikilosakos petaloides* Watson and *Oldhamina decipiens* (de Koninck) as figured by Noetling (1905) the left adductor scar is rudimentary compared with the right adductor and the right diductor appears to have atrophied: this indicates, according to Watson (1917, p. 215), that the brachial valve was moved laterally rather than dorsally in response to diductor contraction, although such movement must have been impossible in those oldhaminids having convex pedicle valves.

In general it is safe to assume that the oldhaminid musculature was degenerate to a degree of almost total atrophy and, although muscle fibres probably separated the epithelial layers of the mantle infold enveloping the internal plate, it is likely that the brachial structures were never elevated or slewed laterally as in normal brachiopods. This lack of movement was not detrimental to the living animal: the internal plate was elevated above the floor of the pedicle valve by the septal apparatus: a steady flow of nutrient water, circulated by the lobated lophophore, could have entered the brachial cavity by way of the distal ends of the lateral lobes and left by the median incision.

MORPHOGENY OF THE OLDHAMINID SEPTAL APPARATUS

The development of the septal apparatus in the oldhaminid pedicle valve corresponding to the lobation of the internal plate has been fully discussed by Fredericks (1925) and Wanner (1935) and needs but a brief review here.

In the primitive *Poikilosakos* a low ridge (flange of Watson, 1917), lying well within the pedicle valve margin completely surrounds the median area of the interior. The flange is roughly subcircular in outline and is indented to form a median loop only, but in adult forms the outline is more irregular, the flange being thrown into a small number of asymmetrically disposed lateral loops in addition to the median one. These loops are not greatly constricted and consequently include medianly a narrow strip of the valve floor bounded by an indented segment of the

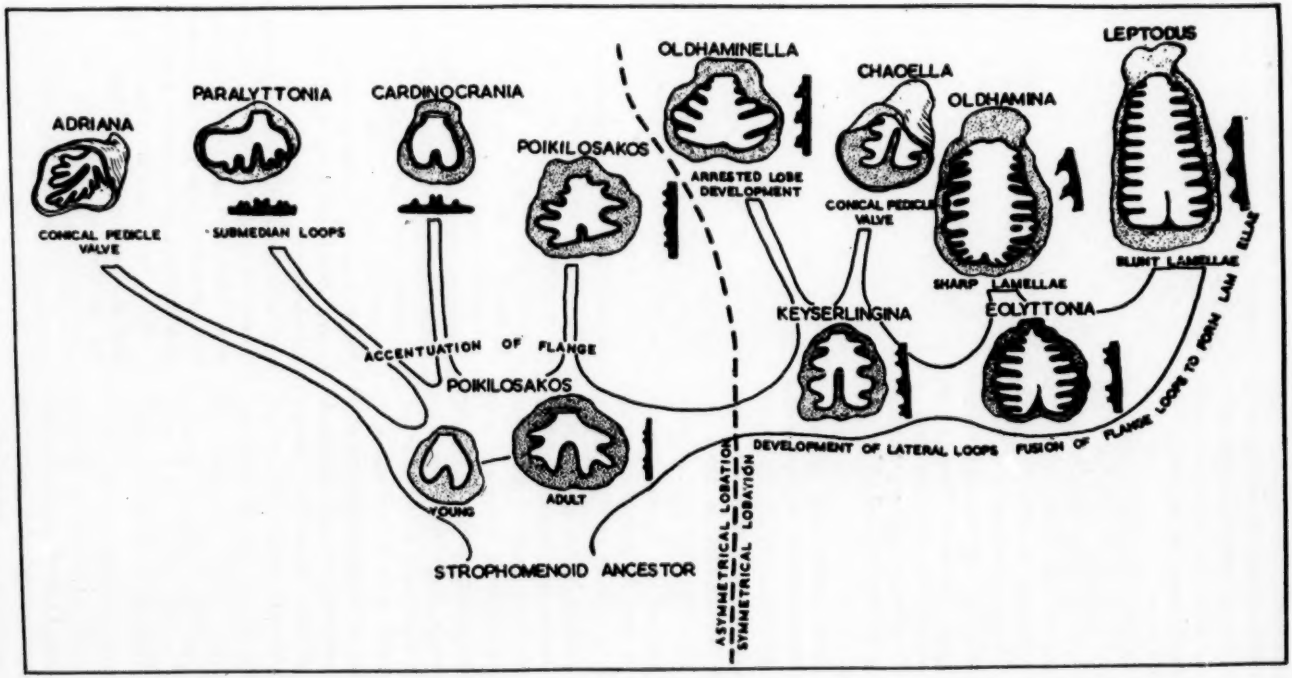

PLATE 3

Diagrammatic representation] of oldhaminoid morphogeny; the profile of a representative portion of the loop or septal development in the pedicle valve of a genus is colored black.

flange. The internal plate of the brachial valve corresponds in outline to the disposition of the flange so that it is irregularly lobate and lies so close to the pedicle valve that each lobe is seemingly isolated distally from its neighbour by a loop of the pedicle valve.

In later oldhaminids like *Keyserlingina* and *Paralyttonia* the loops begin to close by an increase in the size of the flange boundaries and their encroachment onto the median strip of the valve floor until in extreme forms like *Oldhamina* and *Leptodus* the flange boundaries to each loop are completely united into one solid septal structure. In this manner the looped flange of the earlier and more generalized oldhaminids is transformed into a series of variously fashioned septa constituting the septal apparatus of more specialized stocks.

These views on the evolution of the septal apparatus are generally accepted but there seems to be disagreement on the systematic value of the modifications resulting from loop and septal morphogeny (see Wanner, 1935, pp. 265 et seq.) which appear to have been gradually introduced during the ontogeny of the various stocks as well as phylogenetically. Thus in one specimen of *Leptodus* from the Permian of Texas the high sharp septa of the earlier formed posterior region of the septal apparatus are replaced by lower, weaker septa in the later stages of growth, and the initially undifferentiated interseptal strips of the valve floor become elevated into low broad ridges in the anterior part of the shell. These changes were first introduced at the distal ends of the earlier formed septa and gradually encroached anteriorly on to the median line as the animal grew, in such a way that the changeover, which is quite sharply demarcated, occurred along a front convex to the anterior and roughly concentric with the growing edge of the valve.

Other modifications usually associated with the evolution of the septal apparatus included an increase in the number of septa and a closing up of the median incision of the internal plate; but the most important appears to have been a reorganisation of the disposition of loops and septa so that during Permian times two main stocks existed—one characterized by asymmetry the other by symmetry in the development of loops and septa.

OLDHAMINID CLASSIFICATION

The placing of the oldhaminids within the framework of the existing brachiopod classification has been a matter of considerable speculation. Fredericks (1925) considered the group to be derived from the productid *Marginifera*, but more accurate comparative morphology has caused the rejection of this belief. Other paleontologists including Waagen and Wanner have been impressed by the apparent similarity (especially in lobated nature of the lophophore support) between the oldhaminids and the thecideids, and have considered them to be related groups. Both Watson and Noetling, however, have attributed the superficial likenesses to convergence and thus have regarded the stocks to be entirely independent, an opinion supported by the writer.

The various opinions expressed on the affinities of the oldhaminids is a reflection of the profound morphological differences separating them from all other brachiopods, and while most paleontologists place them within the strophomenoids no cogent reason has yet been put forward for allocating them either to the Strophomenoidea or to the Productoidea. That they are strophomenoids is left in little doubt when reference is made to the pseudopunctate shell, the absence of a functional pedicle and the presence of a bilobed cardinal process. But it is impossible to recognise in any of the Upper Carboniferous productoids and orthotetaceids any one stock displaying the characteristic oldhaminid features apart from the ordinal characters listed above. In view of these fundamental differences and the consequent unique nature of the oldhaminid morphology it is proposed to erect a new suborder Oldhaminoidea to embrace *Oldhamina* and its associates.

The oldhaminoids include a wide variety of forms (Pl. 3) but appear to be divisible, as a result of a basic and early divergence, into two distinct suprageneric groups dependent upon the disposition of the septa and loops and it is proposed to recognise these differences by the erection of a new family, Poikilosakidae, in the manner described below.

OLDHAMINOIDEA, n. suborder

Pseudopunctate brachiopods without a functional pedicle, usually cemented throughout ontogeny, shell surface without radial ornament,

shape often highly irregular. Brachial valve vestigial occupying a small posterior triangular area of a large plate of fibrous calcite presumed to have been deposited by an infold of the mantle and to have given support to a ptycholophous or more usually a schizolophous lophophore. Pedicle valve extending posteriorly as an enormous flap intimately connected with the pedicle valve apically and posterolaterally and invariably retroflexed along a narrow median zone lying immediately dorso-posteriorly to the brachial valve, posterior flap highly variable in form, usually the principal organ of fixation and moulded to the base affording anchorage, less frequently strongly retroflexed to come in contact with the external surface of the apical part of the pedicle valve or growing anteriorly and ankylosed to the sides of the pedicle valve to form with it a deep cone. In early stocks the median area of the pedicle valve interior surrounded by a low ridgelike flange indented to form a median loop and a variable number of lateral loops; in later stocks the sides of loops coalesced to form solid septa; internal plate of brachial valve lobated to correspond to the loops or septa. Upper Carboniferous to Permian.

Family OLDHAMINIDAE Schuchert and LeVene, 1929

Oldhaminoids with the loops or septa and hence the lobation of the brachial internal plate symmetrically disposed about the median line. Upper Carboniferous to Permian. Type genus *Oldhamina* Waagen.

POIKILOSAKIDAE, n. fam.

Oldhaminoids with the loops or septa and corresponding lobes of the brachial internal plate developed in an irregular fashion. Upper Carboniferous to Permian. Type genus *Poikilosakos* Watson.

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ENTOMOLOGY.—*Additional material on the phylogeny and dispersal of* Atopsyche (*Trichoptera: Rhyacophilidae*).[1] HERBERT H. ROSS, Illinois Natural History Survey, Urbana, Ill.

The intermingling of elements of South American and North American biotas across the Central American region is a study full of fascination. The fossil record for any terrestrial group in this critical area is very scanty, so that pertinent evidence from biogeography may be our best source of information on certain phases of the subject for some time to come.

Since Dr. King and I prepared our first paper on the dispersal pattern of the genus *Atopsyche*, known only from this area, I have been fortunate in obtaining several additional lots of material and in being able to study the type of *A. implexa* (Navas). Although the new material adds only eight species to the 21 previously analyzed, it brings out several points of biogeographic interest. These fit well the concepts and postulates set forth in the earlier paper on the genus (Ross and King, 1952, Ann. Ent. Soc. Amer. **45:** 177–204) extending some ideas and suggesting modifications of others.

In the first place, the new species *ulmeri* from Peru is a close relative of *cira* from Costa Rica and demonstrates a spread of this otherwise northern group from Central America into South America. This was probably a post mid-Pliocene dispersal.

[1] This study was aided by a grant from the John Simon Guggenheim Memorial Foundation.

it was originally suggested that at this time two South American lines spread into North America, and we wondered why we had no evidence of a complementary spread of a North American form into South America. Here it is.

Two items concern the *ikonnikovi* complex, here renamed the *kingi* complex. We thought this complex originated in South America in the Miocene, but had no really primitive South American species as evidence. The new species *kingi* from Peru proves to be such a primitive member. In addition, a new subgroup of the *kingi* complex has been discovered, typified by a pair of curious, setose,-oval bodies on the third and fourth tergites of the males, fig. 5*C*. This subgroup contains three known species—a primitive one, *vatucra*, from Peru; a more specialized species, *banksi*, from Colombia; and the hitherto misplaced species *implexa* from Costa Rica. This distribution pattern complements that of the *kingi*, *dampfi*, and *boneti* triad.

A fourth point is the finding of a very primitive member of the *batesi* group in Peru, the new species *alconura*. It was postulated on phylogenetic evidence that this line originated from South American ancestors, although the known members came from Mexico and the West Indies. The discovery of a primitive form, *alconura*, in Peru suggests that the progenitor of the group may have differentiated in South America before dispersing to other areas.

The other two new species involve no controversial points. *A. explanata* from Peru is a close relative of *kamesa*, from Bolivia. *A. serica* from Brazil is the most primitive member yet known of the *longipennis* group, and emphasizes the relationship between the different lines within the group.

Unless otherwise stated, types of the new species are deposited in the collection of the Illinois Natural History Survey.

Subgenus **Atopsyche** Banks

The opportunity to study the type male of *Ventrarma implexa* Navas, the genotype of *Ventrarma* Navas, shows that it is a member of the typical subgenus *Atopsyche* and not a member of the group considered as the distinctive subgenus *Ventrarma* by Ross and King, 1952. *Ventrarma* must therefore be placed as a synonym of the subgenus *Atopsyche*. A new name, *Atopsaura*, is proposed later in this paper for the other segregate.

Atopsyche ulmeri, n. sp.

Male.—Length 5.5 mm, front wing 5 mm. Color light brownish yellow with darker areas on the mouthparts, front legs, and thorax; wings variegated with irregular light and medium spots of brown. General structure typical for genus. Abdomen with third tergite bearing a faint basal band of minute setae, fifth sternite with a small dorsal projection near base of segment. Male genitalia as in Fig. 1. Paracercus elongate with a high sharp point in middle, apical portion elongate, narrow, and curved sharply laterad at apex. Filicercus short, with a few setae at or near tip. Clasper very elongate and slender, with apical segment short, hooked at apex, with the ventral margin rounded. Aedeagus short and broad, with a narrow lateral flange.

Holotype.—Male, Paucartambo, Ccosnipata Valley, Cusco, Peru, November 15, 1951, Felix Woytkowski. *Paratypes.*—Same data, but November 26, 1951, 3♂.

This species is most closely related to *cira* (Mosely), differing in the slender apex of the paracercus and the undivided apex of the aedeagus.

Atopsyche explanata, n. sp.

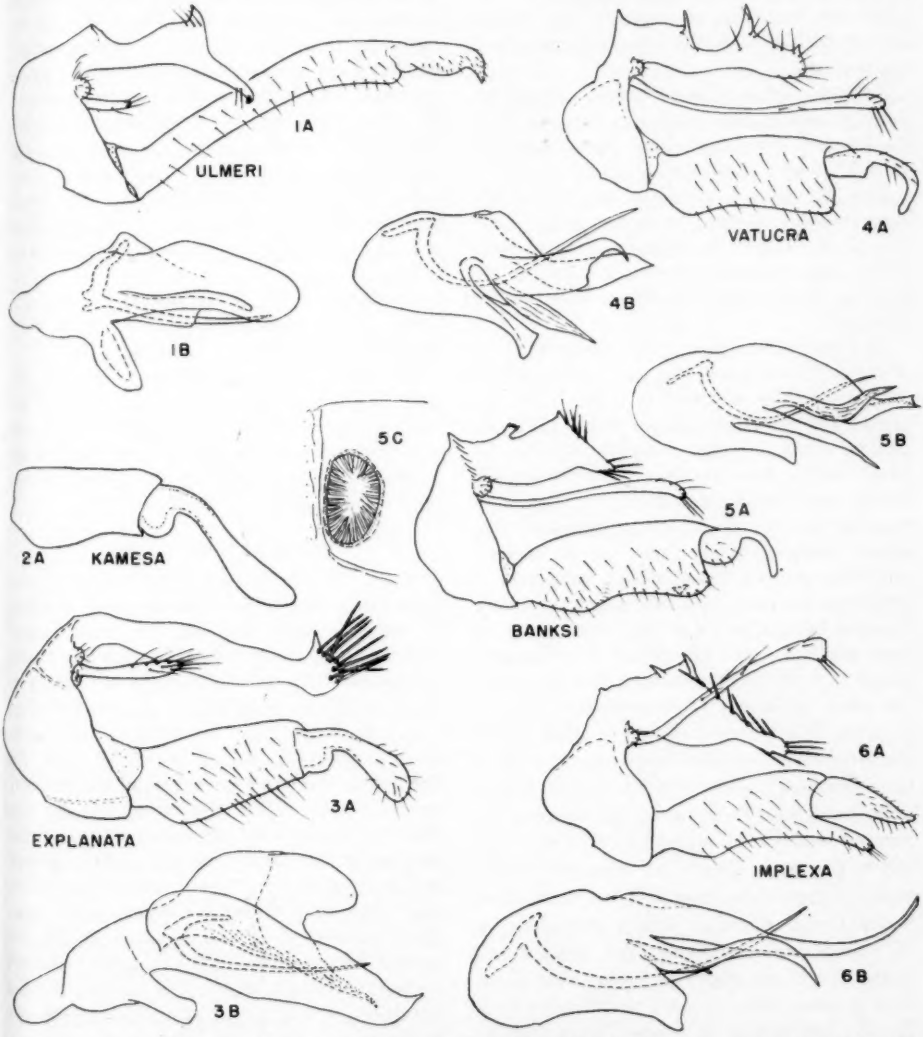
Male.—Length 7.5 mm, front wing, 7 mm. Color yellowish brown below, darker brown above, the wings a light shade of chocolate brown. Abdomen simple, without setal bands on segment three and with only a small process on the fifth sternite. Male genitalia as in Fig. 3. Paracercus slender and elongate, apparently with only the apical point, and bearing at the apex a cluster of long, stout setae. Filicercus of moderate length, with an irregular scattering of setae on the apical half. Clasper with basal segment twice as long as wide, apical segment slightly more than half length of basal one, curved and constricted in middle so as to form a clavate apex and a bulbous base. Aedeagus with a large, high, bilobed central portion, and produced on each side of this into a wide, upcurved flange. In repose the paracercus fits between the flange and the central high portion of the aedeagus.

Holotype.—Male, Paucartambo, Ccosnipata Valley, Cusco, Peru, November 17, 1951, Felix Woytkowski.

This species is a close relative of *kamesa* Ross and King, differing in the shorter apical segment of the clasper and the shallower lateral flange of the aedeagus. The true division between the two segments of the clasper is sometimes difficult to see and in the original description of *kamesa* was not truly shown. A corrected drawing of the clasper of *kamesa* is included here for reference, Fig. 2*A*.

Atopsyche kingi, n. sp.

Male.—Size and color almost identical with the preceding except that the color is slightly darker and the tibiae and tarsae are covered with brownish hair. Abdomen with third tergite bearing an irregular, somewhat oval, corner patch of minute hairs on anterolateral angle;



FIGS. 1–6.—Male genitalia and associated structures of *Atopsyche*: *A*, Genital capsule, lateral aspect; *B*, aedeagus, lateral aspect; *C*, oval body on fourth abdominal tergite.

this same corner of the segment on the third and fourth tergites is produced into a short internal sclerotized band ending in a broader, rounded apex, Fig. 7*F*. Fifth sternite with only a short process. Genitalia as in Fig. 7. Paracercus with a high middle projection and a lower point at apex. Filicercus elongate and clavate. Clasper with basal segment moderately long and stout, with a somewhat angulate mesal shoulder near middle; apical segment short, broad, and curved ventrad at tip. Aedeagus with apical portion divided into two pairs of processes, the ventral pair shorter and dark, the dorsal pair longer and asymmetrical.

Holotype.—Male, Paucartambo, Ccosnipata Valley, Cusco, Peru, November 27, 1951, Felix Woytkowski. *Paratypes.*—Same data, including dates November 20, 26, and 27, 17♂.

This species is a primitive member of the *kingi* complex differing from the other members of the complex in lacking the basal tooth on the paracercus and from other species of the genus in the elongate pair of processes on the aedeagus.

The internal straplike appendage at the base of the third and fourth tergites is a most useful character in this complex. It occurs in all the members of the *kingi* complex which are available for study. In these complexes also the internal rod appears to have moved from the ventral end of the basal angulation to the dorsal end, and the apex of the aedeagus is divided into several foliatious lobes. These are at variance with the available description of *ikonnikovi*, in which the internal rod of the aedeagus is illustrated as being attached at the ventral end of its basal angulation, and the apex of the aedeagus is simple as in the *bolivari* complex. For this reason the exact placement of *ikonnikovi* is open to question. If it is indeed related to *kingi* and its relatives, then *ikonnikovi* would seem to be a more primitive member of the same line. On the other hand the two pre-apical processes on the paracercus are most unusual in that the basal one is the larger instead of being the smaller as in members of the *kingi* complex. Until actual material is available for study, *ikonnikovi* can be placed only tentatively, and perhaps best at the base of the *kingi* line. Under these conditions it seems better to use a new complex name for the aggregation of species *boneti*, *dampfi*, *kingi* and the three following, and I am using the term *kingi* complex, naming it after the most primitive known member.

Atopsyche vatucra, n. sp.

Male.—Length 6.5 mm, front wing, 6 mm. Color identical with the preceding, being a moderately dark brown for the genus. Abdomen with tergite three and four each bearing a curious oval body, Fig. 5*C*, on the antero-lateral corner of the tergite, and also the internal spatulate strap as in Fig. 7*F*; process of fifth sternite small. Genitalia as in Fig. 4. Paracercus with three points, the middle one large and high, the basal one smaller and spur-like, the apical one small. Filicercus elongate and slightly clavate. Basal segment of clasper almost rectangular, the ventral margin slightly incised and the apico-dorsal corner slightly produced on the mesal side; apical segment with the apical portion slender, finger-like and hooked. Aedeagus with three pairs of lateral processes as shown in Fig. 4*B*.

Holotype.—Male, Paucartambo, Ccosnipata Valley, Cusco, Peru, November 26, 1951, Felix Woytkowski. *Paratypes.*—Same data, 2♂.

This and the following two species form a distinct subgroup of the *kingi* complex in which the third and fourth abdominal tergites have the odd oval bodies shown in Fig. 5*C*. Of the three, *vatucra* is the most primitive as shown by the three distinct points on the paracercus.

Atopsyche banksi, n. sp.

Male.—Length 10 mm, front wing 9.5 mm. Color fairly dark brown with the usual mottling of various colored hair on the front wings. Abdomen with structures of the third and fourth tergites and fifth sternite identical with the preceding. Genitalia as in Fig. 5. Paracercus trianguloid, the apical point not evident, the middle point small but on a high triangular crest, the basal point short and stubby, its tip divided into several minute points. Filicercus elongate and clavate. Clasper with basal segment somewhat rectangular, the ventral margin slightly incised, and bearing a short mesal pointed projection near apex and a broad shoulder near base; apical segment with basal portion round, apical portion narrow, fingerlike, and curved sharply ventrad. Aedeagus with apical portion divided into three pairs of lateral lobes shaped as shown in Fig. 5*B*.

Holotype.—Male, San Antonio, Colombia,

1,800 meters elevation, February, Fassl. coll. (Museum of Comparative Zoology).

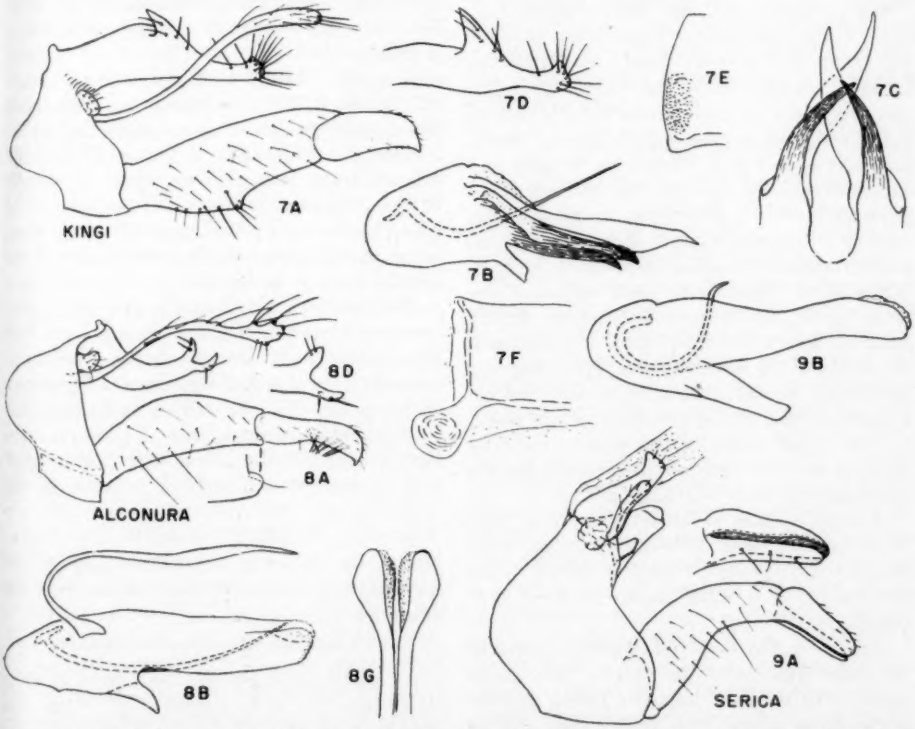
This species is a close relative of *vatucra*, the two being obviously grouped together on the basis of the odd clasper. From *vatucra*, *banksi* differs in the shape of the point on the paracercus and the lobes of the aedeagus.

Atopsyche implexa (Navas)

Thanks to the courtesy of officials of the Paris Museum, the type male of this species was studied in detail and compared with a second specimen, also labeled "Costa Rica" which was identical with the type and was made available for further study. To supplement the original description the following is added, together with illustrations of parts in Fig. 6.

Male.—Length 8 mm, front wing 7.5 mm. Structures of abdominal tergites three and four and sternite five, identical with those of the preceding two species. Male genitalia as in Fig. 6. Paracercus high and trianguloid, with no apical point but with middle and basal points spurlike. Filicercus elongate and almost clavate at apex. Clasper fairly broad, with apico-ventral corner produced into a long fingerlike projection which extends two thirds along the apical segment; apical segment almost triangular but also sinuate, tapering to a sharp point. Aedeagus with three pairs of lateral processes, the upper pair very long, the middle pair fairly long, and the ventromesal pair very short and scarcely visible from lateral view.

The resemblance of the clasper to that of *majada* is quite striking, and on this evidence alone the species was originally considered a possible close relative of *majada*. Details of abdominal tergites three and four, of the various structures of the aedeagus, and the paracercus, however, demonstrate clearly that this species is not at all close to *majada* but instead belongs in the *kingi* complex.



FIGS. 7–9.—Male genitalia and associated structures of *Atopsyche*: *A*, Genital capsule, lateral aspect; *B*, aedeagus, lateral aspect; *C*, apex of aedeagus, ventral aspect; *D*, apical portion of paracercus, ventrolateral aspect; *E*, anteroventral corner patch on fourth abdominal tergite; *F*, inner view of opposite anterior corner showing spatulate process; *G*, apex of aedeagus, dorsal aspect.

To date this species is known only from the type, bearing the data "La Caja, Costa Rica, Paul Serre 1920," and specimen here studied, labeled "Costa Rica."

Atopsyche dampfi Ross and King

Previously known only from Mexico, a record for another country may be added: Rosario Mines, Honduras, April 30, M. Bates, 1 male. (Museum of Comparative Zoology)

Subgenus **Atopsaura,** n. subgen.

As explained earlier, the genotype of *Ventrarma* actually does not apply to the group which was called the subgenus *Ventrarma* by Ross and King. For this latter segregate I am proposing the name *Atopsaura*. The genotype is hereby designated as *Atopsyche hamata* Ross and King.

Atopsyche alconura, n. sp.

Male.—Length 6.5 mm, front wing 6 mm. Color fairly light brown, intermediate between the yellowish brown of *ulmeri* and the darker brown of the other species. Abdomen with tergite three having a very faint basal band of minute hairs, and with process of fifth sternite small. Genitalia as in Fig. 8. Paracercus elongate and curved dorsad, the apex divided into two sharp processes, with no projections basad of these. Filicercus elongate; its apex is almost capitate, and is irregular due to the wartiness of the bases of the setae. Clasper with basal segment somewhat bowed, its apico-ventral corner slightly produced into a rounded extension overlapping the corner of the apical segment, apical segment moderately slender, largest in middle, the extreme apex produced into a short ventral point, and the mesal margin armed with several long sharp setae. Aedeagus simple, except for the dorsal spine typical of the *batesi* group.

Holotype.—Male, Paucartambo, Ccosnipata Valley, Cusco, Peru, November 26, 1951, Felix Woytkowski. *Paratype.*—Same data, 1♂; Cangallo, south Peru, 2,600 meters elevation, 1♂ (Hamburg Museum).

Judged by the short apicoventral process of the basal segment of the clasper, this species seems to be the most primitive known member of the *batesi* group. It is readily distinguished from the other members by this character and by the curious bifurcate tip of the paracercus.

Atopsyche serica, n. sp.

Male.—Length 8.5 mm, front wing 8 mm. Color dark brown with the usual mottling. Abdomen without special structures on the third and fourth tergites and with only a small process on the fifth sternite. Genitalia as in Fig. 9. Paracercus very short, directed more dorsad than posteriad, and with neither middle nor basal point. Filicercus slightly shorter, fingerlike. Ventrad and mesad of these two structures is a short thumblike projection. Between the filicerci and below the tenth tergite is a curious horseshoe-shaped structure beneath which the aedeagus protrudes. In lateral view this appears as an inconspicuous hoodlike structure between the paracerci. Basal segment of clasper bowed and directed more dorsad than usual; its ventral mesal margin is apparently produced into a long, narrow flange which extends along the inner side of the apical segment, which is grooved to receive it; apical segment elongate, oval, widest near base, and rounded at apex. Aedeagus very simple, the internal rod coiled as in *longipennis*.

Holotype.—Male, Nova Teutonia, Brazil (27°11′ B, 52°23′ L) October 4, 1939, Fritz Plaumann (Museum of Comparative Zoology).

This species is closest to *longipennis* but the claspers are a little more suggestive of *hamata*. It is distinguished from all other members of the group by the extra pair of short lateral processes below the filicercus and the sclerotization of the structure above the opening for the aedeagus.

This species emphasizes the unusually rapid rate of morphological differentiation which has occurred between species of the *longipennis* group in contrast with the species of other groups in the genus. It is also interesting to note that in this species unusual pairs of processes have been added which are reminiscent in both position and appearance of structures in some of the Australian and New Zealand genera which are only distantly related to *Atopsyche*. This demonstrates the tendency toward the parallel development of similar genitalic structures in the tribe.

Atopsyche falina Ross and King

An additional record has been received from Argentina, the only country for which this species is known: El Tuncho Catanarca, Argentina, 2500 meters elevation, May 5, Jorgansen, 2♂ (Museum of Comparative Zoology).

Atopsyche mexicana (Banks), n. comb.

Philopotamus mexicanus Banks, Trans. Amer. Ent. Soc. **27**: 370. 1901.

The type, in the Museum of Comparative Zoology, was examined in 1951 and found to be without abdomen, so that it is not possible at present to identify the specimen beyond genus. The venation indicates definitely that it belongs to *Atopsyche*.

Atopsyche callosa (Navas)

I had an opportunity to study the type in the Paris Museum. Although labeled and recorded in the original description as a male, the specimen actually is a female, and could not be identified except to genus.

ORNITHOLOGY.—*Feeding adaptations and systematics in the avian order Piciformes.* WILLIAM J. BEECHER, Chicago Natural History Museum. (Communicated by Herbert Friedmann.)

Recently Dr. Herbert Friedmann offered for my study some spirit specimens of honeyguides (Indicatoridae), together with other members of the order Piciformes. It was hoped that such an investigation as I carried out for the Neotropical honeycreepers (Beecher, 1952) might cast further light on both the feeding adaptation and systematic position of these birds so well studied by Friedmann (in MS.). Checking the systematic position of the honeyguides required a somewhat hasty completion of a long-time survey of jaw musculature in the class Aves which I will publish elsewhere. The present paper simply deals with the food adaptations in the head region of the piciform honeyguides, barbets, puffbirds, jacamars, toucans, and woodpeckers, which seem to occupy an interesting position between the perching birds (Passeriformes) and the remaining avian orders. Specimens used are from the collections of the United States National Museum and Chicago Natural History Museum. For their use or for advice, I am indebted to Herbert Friedmann, Austin L. Rand, Emmet R. Blake, and D. Dwight Davis.

SPECIMENS EXAMINED

Although a limited number of anatomical specimens was studied, the use of numerous skulls of related species considerably swells the list of material examined. This material is sufficient to suggest very strongly that the same constancy of muscle pattern found to hold for the species of passerine families holds for non-passerine families as well. Species dissected are: (Indicatoridae) *Indicator minor conirostris, I. exilis, I. maculatus, I. minor minor;* (Ramphastidae) *Pteroglossus torquatus, Ramphastos cuvieri, Selenidera spectabilis;* (Capitonidae) *Lybius leucocephalus, Megalaema haemacephala, M. rafflesii, M. zeylanica, Trachyphonus purpuratus;* (Bucconidae) *Chelidoptera tenebrosa;* (Picidae) *Colaptes auratus, Dryocopus pubescens, Melanerpes carolinus, M. erythrocephalus, Piculus chrysochloros, Picumnus squamulatus.* No specimens of jacamars were on hand to dissect, unfortunately, but skulls strongly suggest their close alliance with the barbets.

INVESTIGATION TECHNIQUES

In undertaking this study I have pursued essentially the plan laid out in my paper mentioned above and in the more comprehensive work on the phylogeny of the Oscines (Beecher, 1953). This consists in comparing various systems throughout the groups considered, as illustrated in the figures for the families. In each of these the jaw musculature is illustrated in side view and oblique view (with eye removed), as indicated in black on the accompanying skull drawings. The tongue is drawn on the right above and the ectethmoid plate with its foramina (separating the orbital and nasal cavities), on the left. In the center is figured the horny palate pattern and the bill. The logic behind the comparison of systems is that it should be possible in an avian order to establish a ground plan from which the groups (families) are adaptively specialized. Special emphasis was placed on jaw muscle pattern as a family trait in the Oscines because song-bird families appear to be diverging from such a ground plan under the selection pressure of different food types and because each family tends to have a very constant pattern. In the present

order the muscle patterns seem to exhibit conservative differences between the families that prove ideal both for emphasizing their adaptive differences and at the same time encompassing them within the diagnosable ground plan of Piciformes. The other characters illustrated serve to safeguard against erroneously including a convergent species, occasionally possible if a single character is used blindly—and to further point up functional differences between the families in these less conservative parts. These systems will now be taken up below to see how well they support the current ornithological opinion that the piciform families are closely related and to show the extent to which they are differently adapted for food-getting.

THE JAW MUSCLE PATTERNS

No systematic account of muscle origins or insertions will be included here. This is well covered in Moller (1931) and Fiedler (1951); the abbreviated account in Beecher (1951b) should suffice for the understanding of muscle function stressed in the present paper since the same muscles are concerned.

A strong facies resemblance between the jaw muscle patterns of the piciform families persists through their quite different food adaptations, which constitutes one of the best arguments for close relationship. The far posterior position of the flattened pterygoid bones where they articulate with the palatines along the sphenoidal rostrum causes *M. pterygoideus dorsalis posterior* (*M3b* in Figs. 1 and 2) to be nearly obscured from view, suggesting relationship with Trogoniformes and Coraciiformes. *M. pterygoideus dorsalis anterior* (*M3a*) is correspondingly enlarged to make up the needed power for retracting the pterygoids, its broad insertion on the sphenoidal clasp, formed by the articulation of the palatines and pterygoids, covering *M. pterygoideus ventralis posterior* (*M4b*). The functional result is unusual emphasis on palate retraction in the kinetic bills of all of these families. Since this retraction is translated by the nasofrontal hinge into a downward drag on the upper mandible, the unusually heavy construction of this part is clearly functional in feeding. Along with this is a considerable emphasis on the adductors. In Capitonidae and Ramphastidae *M. pseudotemporalis profundus* (*M5*) is powerfully developed for dragging on the orbital process of the quadrate and rocking this important bone backward on its articulation with the cranial part of the skull, initiating palate retraction and adduction of the upper mandible.

This emphasis on the palatine retractors and the adductors is about proportional to the mass of the bill in the several families studied. In Capitonidae, and particularly in *Lybius* with its stout, notched bill, *M. pterygoideus ventralis posterior* (*M4b*) originates all along the outer surface of the mandibular ramus posteriorly, as well as on the customary inner surface. This is also noted in Ramphastidae and Picidae in progressively lesser degree (the former with *M4a* and *b* fused) but not in Indicatoridae. The adductors are also most strongly stressed in the Capitonidae and Ramphastidae, the temporal slip of *M. adductor mandibulae externus superficialis* (*M7a*), particularly, showing a deep incursion to the dorsal midline of the skull posteriorly. This is not met with in the Oscines but is characteristic of the Suboscines and a vast majority of other avian orders.

The Picidae have a good expression of both palatine retractors and adductors but are outstanding for the extreme emphasis on the protractors of the mandibles, *M. depressor mandibulae* (*M1*) and *M. protractor quadrati* (*M2*). This is especially so in the latter, which originates over most of the area of the interorbital septum which (unlike most birds) is thoroughly ossified in woodpeckers to protect the brain and unusually ossified in the other piciform families. This arrangement, which is met in the piculets as well as in the more highly-adapted woodpeckers, is also found among passerines in the nuthatch *Sitta*. Its effectiveness in prying is evident, and it is seen (with *M2* less well expressed) in numerous species of prying birds (Beecher, 1950; 1951a and b); but in woodpeckers it probably serves as part of an interesting shock absorbing mechanism. I disagree with Burt (1930) that the woodpecker bill is immovably joined to the skull in even the most highly adapted forms. The only unkinetic bird skull is seen in the lizard-like subclass Archaeornithes. In all other birds the upper mandible joins the skull at the naso-frontal hinge and the jugal-palatopterygoid armature joins its base to the quadrate in a frame that slides along the sphenoidal rostrum under the control of the jaw musculature. The key bone in this process is the movable quadrate which permits these antero-posterior movements of the armature to be translated into elevating and depressing movements of the upper mandible

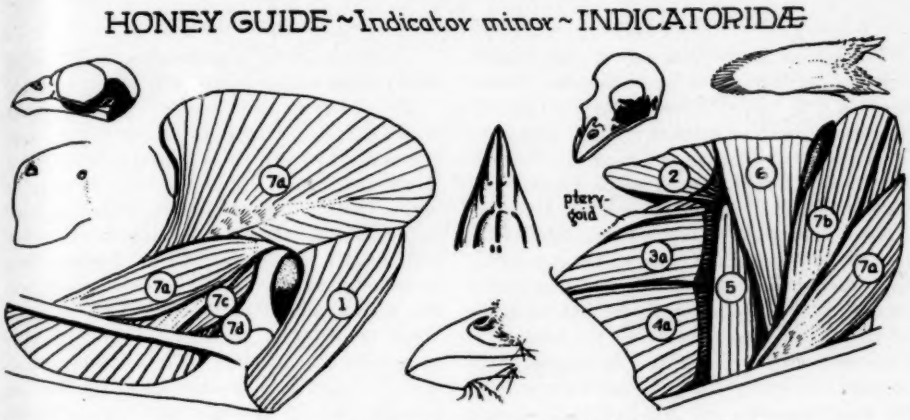


FIG. 1.—Detail drawing of jaw muscle pattern of the honeyguide (Indicatoridae).
Protractors. 1 depresses the lower mandible; 2 elevates the upper mandible.
1. *M. depressor mandibulae*
2. *M. protractor quadrati*
Palatine retractors. Combined action draws upper mandible downward.
3. *M. pterygoideus dorsalis:* a) *anterior;* b) *posterior* (underlies 2)
4. *M. pterygoideus ventralis:* a) *anterior;* b) *posterior* (underlies a)
5. *M. pseudotemporalis profundus*
Mandibular adductors. Combined action draws lower mandible upward.
6. *M. pseudotemporalis superficialis*
7. *M. adductor mandibulae:* a) *externus superficialis;* b) *externus medialis;* c) *externus profundus;* d) *posterior*

In the shock-absorbing mechanism of woodpeckers and nuthatches the antagonistic action of the enormous *M2* against the retraction of the pterygoid musculature probably holds the bill in a state of resilient rigidity as it rains its blows on a tree trunk. Woodpeckers also have a special nasal mucous gland (Technau, 1936); this is visible in the floor of the orbit just ventral to the ectethmoid plate and is less well expressed in sapsuckers (*Sphyrapicus*) than other genera. Since this may serve to trap dust raised by pecking (an occupational hazard of woodpeckers like silicosis among humans!) sapsuckers, habitually working soft, green wood, may not need it so much. This has nothing to do with the enormous sub-lingual mucous gland which serves to make the woodpecker tongue sticky.

The Indicatoridae, strange to say, show no specializations of the jaw musculature or salivary glands at all. The bill, too, is more generalized than that possessed by any other piciform family, except for the unusual feature that the tips of the peculiarly blunted mandibles meet without notable overlap of the upper—an adaptation, possibly, for biting off bits of wax and honey. But the general facies of the order is recognizable in the jaw muscle pattern which is more generalized than in any of the other families. This is clearly seen in the simple *M. pseudotemporalis superficialis* (*M7*) which, in the other families, shows a slight approach to the Suboscines and to Coraciiformes and possibly Trogoniformes. The honey-guide musculature is, in fact, the nearest seen in any of these families to the ideal ground plan for the order. This is not to state that this family is actually ancestral to the others but only that it may more nearly resemble the less specialized common ancestor. In other respects I am inclined to think the basic stock might have been more like the barbets but these have now, in process of developing a massive musculature for power, sheathed much of the musculature in tough aponeuroses to which shorter fibers fuse in semblance to the pinnate muscles so important in the higher Oscines. This is an arrangement found in primitive oscinine shrikes like Cracticidae, Prionopidae and Vangidae. The only muscles that could class as pinnate in Piciformes are the temporal slip of *M7a* and *M7c*. This supports the general opinion as expressed in Wetmore (1940; 1952) and in Mayr and Amadon (1951) that the group is somewhat more primitive than Passeriformes.

THE TONGUE

The tongue is not generally a very reliable index of relationship in birds (Beecher, 1951a) because it is apparently so readily modified in conjunction with an extreme feeding adaptation. This is true in Piciformes. The tongues of barbets are the generalized tongues of insect eaters, not distinguishable by any reliable characters from those of some passerine insect eaters, except that, like the other piciform families, the papillae of the posterior surface of the tongue are unusually abundant. The moderately frayed out horny tip is unspecialized in barbets and the tongues of honey eaters are very similar. The tongues of the toucans are simply elongate and narrow, with the fringe extending well posterior; such a tongue would be useful in lapping juice from pulpy fruits as well as in the usual process of biting out pieces. The woodpecker tongue is so vastly modified from the ground plan of the order that little external evidence of relationship remains here. The frayed horny fringe is directed backward as a battery of barbs and the papillae of the posterior border are directed inward to permit withdrawal of the tongue within a skin sheath. The long hyoids of woodpeckers and the great extensibility of the tongue need no special description.

HORNY PALATE

The horny palate is in large measure dependent on the tongue and does not always provide direct evidence of relationship where adaptive re-arrangement has been extensive, as in the Picidae. In the other four families dissected there is a notable resemblance in the thin cutting edge of the tomium in the upper mandible, combined with the vaulting of the palate itself. This is so pronounced that little evidence of a lateral palate ridge, generally present in passerines, can be seen. The central ridge is strong in all families. Posterior palate relief is rather non-descript.

ECTETHMOID PLATE

The ectethmoid plate is convincingly similar in all of the piciform families and all have the foramen double. This condition is considered advanced in my work on the Oscines, primitive forms having a single foramen which is larger the more primitive they are. In Galliformes, a possible ancestor, the foramen may be said to occupy the entire plate which is not closed ventrally at all.

THE BILL

The bill is similar in ground plan in all but the woodpeckers and jacamars, with a very strongly bowed culmen and rather massive upper mandible. The nostril is far posterior, non-operculate and (in honeyguides) raised into a membranous tube. In barbets the bill may be long or short with the tomium sometimes notched as in *Lybius*, a feature that seems to be multiplied with length in the toucan bill. Barbets have abundant narial and chin bristles as do puffbirds, but the elongate, straightened bill of jacamars shows reduction of bristles. Puffbirds generally have narrowed, hooked bills. Toucans, woodpeckers, and honeyguides have the bristles virtually lacking and the bills without hooks, except for a slight tendency in toucans which are also much notched. The toucan bill is, of course, unique in the degree of lightness achieved with its cancellous internal structure.

In connection with the bill the barbets seem to be fruit and insect eaters, often expert flycatchers; puffbirds are lethargic flycatchers; jacamars, graceful and swift flycatchers. Toucans are fruit and insect eaters. Woodpeckers are specialized insect eaters, eating many wood-boring insects, but also anteaters and flycatchers, some taking sap and flower juices as well as fruit. Honeyguides are insect eaters that evidently have become specialized for eating honey and even getting nutrition out of beeswax. This adaptation will be discussed further.

PLUMAGE

Barbets generally have brilliant plumage—barring and streaking on a ground of yellow or green with flashmarks of crimson—which is clearly similar to that of some woodpeckers. Puffbirds, with barred and streaked plumage also, are duller in color and jacamars are more often coppery green and iridescent brown in solid masses. The puffbirds *Nystalis* and *Malacoptila* (and the woodpecker, *Jynx*) resemble owls and nightjars in plumage, the jacamars resemble hummingbirds. This resemblance is not taken as evidence of direct relationship but other lines of evidence suggest that these orders and many others may be springing independently from Galliformes which I am inclined to regard as our most primitive, unspecialized bird stock. Toucans have plumage patterns of solid greens and yellows and reds suggestive of barbets. Honeyguides re-

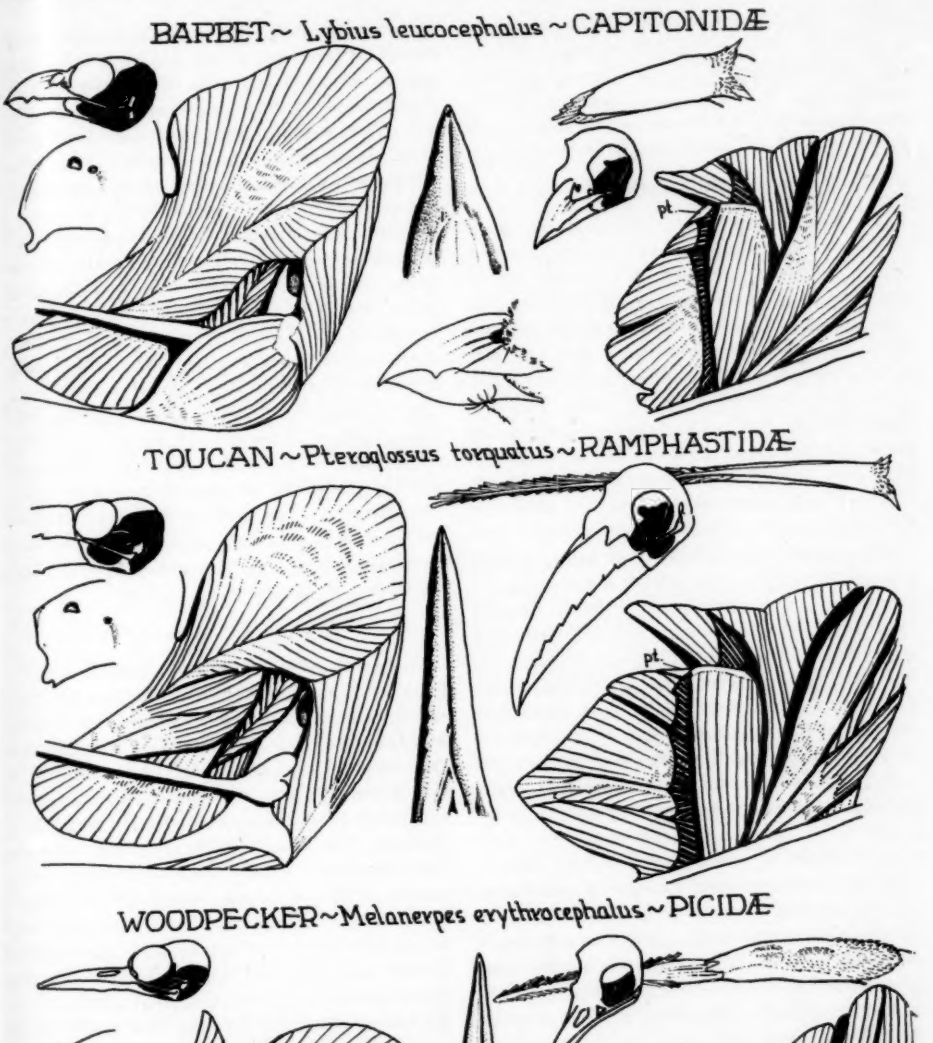


FIG. 2.—Detail drawing of jaw muscle pattern in the barbet (Capitonidae), toucan (Ramphastidae), and woodpecker (Picidae).

semble certain dull-patterned barbets like *Lybius leucocephalus*. On the basis of plumage, in fact, one would be inclined to say that all piciform families may have originated from the barbets. If so, it would have been before the bills became as specialized as they are now, in all probability.

OTHER CHARACTERS

The idea that the barbets may be the ancestral piciform family is supported by other characters which might be preadaptive to traits highly expressed in the other families. All these families have zygodactylous feet in which the second and third toes are directed forward, the first and fourth, backward. This arrangement of toes is particularly advantageous for birds climbing about on tree trunks as barbets and woodpeckers do or for perching. Toucans and honeyguides may have largely abandoned this trait without the toes being under any selection to return to the usual condition. Barbets have many of the woodpecking traits of Picidae with highly ossified interorbital septum, a feature found throughout the order, but especially in Picidae. Barbets excavate holes as do woodpeckers. Toucans nest in hollow trees. Honeyguides are parasitic on hole-nesting birds, often members of Piciformes, according to Bannerman (1933). In the pelvic appendage, the re-arrangement of the toes has resulted in changing the position of tendons and loss of the *ambiens* muscle, considered of important diagnostic value by Garrod (1873).

WAX-EATING IN THE HONEYGUIDES

As to the honey- and wax-eating adaptation in honey guides, no notable specialization of digestive organs was found. There is no sign of enlarged palatine salivary glands such as are found in all the nectar-eating groups of the world (Beecher, 1953)—Dicaeidae, Nectariniidae, Meliphagidae, and the New World hummingbirds and honeycreepers. If only honey were taken this would not be surprising because the bulk of this is immediately assimilable and there would be little need for invertase or any enzyme for breaking down sucrose. But Friedmann (MS.) has evidence that honeyguides are able to derive nutrition from beeswax, implying a rather complex enzyme action. With the specimens available I could carry out only the crudest sort of sampling technique aimed at studying wax digestion. I removed food material from the oral cavity, stomach, and hind gut of the species studied and heated it on a scalpel blade. A wax residue was obtained on the blade from contents so treated of oral cavity and stomach of *I. exilis* and *I. maculatus* in some samples—never from the hind gut. This might suggest wax digestion in the stomach or small intestine were the sampling adequate. As it stands these results are merely suggestive.

This trait of the honeyguides is the more interesting because of their general flair for parasitism. They lay their eggs in the nests of other birds, often close relatives, and they have learned to get animals more capable than themselves to uncover the honey combs they prefer to feed on. They must have started this specialization in habit by leading animals, perhaps the honey badger (*Mellivora*) to hives. Chapin (1939) suspects other mammals, including squirels and monkeys, of aiding the birds in getting at honey. The discovery, apparently only by *Indicator indicator*, that man could be led to bee trees with satisfactory results is necessarily a recent specialization of the trait.

SUMMARY AND CONCLUSIONS

An investigation of feeding adaptations in the head region of the piciform bird families, Capitonidae, Bucconidae, Ramphastidae, Picidae and Indicatoridae, was undertaken to study their morphological and systematic relationships. The jaw muscle pattern shows a strong facies resemblance in all, suggesting that the order Piciformes is a real unit. The honeyguides have the least specialized pattern and may represent the ground plan from which the other families have been derived, though other indications are that the barbets are nearer the ancestral stock. From this ground plan the barbets diverge by having more massive adductors and palatine retractors, the toucans by fusing the slips of *M. pterygoideus ventralis* and sheathing the musculature increasingly in aponeuroses for increased palate retraction. The woodpeckers extend enormously the origins of the mandibular protractors, particularly *M. protractor quadrati*, a powerful antagonist to the muscles of palate retraction, to produce a shock absorber for the bill. The tongue is so far modified in toucans and woodpeckers as to offer little positive evidence of relationship but the horny palate is less modified and the ectethmoid plate is similar in all. Bills and feeding habits suggest close but disjunct relationships in a single series and plumage suggests origin

of piciform families from the barbets or an ancestral group with a somewhat less-pronounced bill. Zygodactylous feet and the hole-nesting habit, taken in combination with the above, support present ornithological thought as to the unity of the order. The trait of honey guides of leading animals to bee hives seems to be part of a general parasitic complex which includes brood parasitism as well. No digestive abnormalities were noted but enzymes for wax digestion may be produced in stomach or small intestine.

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ZOOLOGY.—Psammodesmus, *a neglected milliped genus* (*Polydesmida: Platyrhacidae*). RICHARD L. HOFFMAN, Clifton Forge, Va. (Communicated by H. F. Loomis.)

It is unfortunate that much of the previous work on diplopod taxonomy has been of rather poor quality. Far too often one finds himself obliged literally to revise a genus or tribe before feeling safe in placing an undescribed species. This is precisely the situation I encountered on endeavoring to place a new platyrhacid milliped found in the collections of the U. S. National Museum. Fortunately, however, the problem has been of fairly easy resolution although depending upon some rather extensive nomenclatorial changes. Although the group directly involved is a South American one, it has been necessary to consider the entire family of the Platyrhacidae. This has been made possible by the exceptionally useful treatise by Carl Attems, in Das Tierreich, Lief. 69, 1938. Despite the value of this reference, I believe that Attems's somewhat conservative treatment does not give proper recognition to the numerous species-groups whose characters seem clearly to be of generic level. Attems recognizes a single genus—divided into six subgenera—with the characters which I ascribe to the family Platyrhacidae. (The other six genera of "Platyrhacidae" treated in his monograph are referable to the family Euryuridae in the sense of Pocock and Chamberlin.)

Interestingly enough, the first contribution to the systematics of the tropical American platyrhacids, by O. F. Cook (1896), still appears to provide the most logical arrangement of the species! Cook was the first worker to break up the large widespread genus *Platyrhacus* (*Acanthodesmus* or *Stenonia* of early writers) with the proposal of numerous generic names. His arrangement, although reasonable, was never generally accepted, and the most authoritative recent workers have reverted to the use of the name *Platyrhacus* for the majority of the species. There are, however, within the family a great number of diverse types which, if they occurred in the temperate regions where faunas are better known, would long ago have been recognized as well-marked genera.

Cook's paper "New American Platyrhacidae" (Brandtia, 1896, no. 12) included the diagnoses of nine new American genera. Four of these (*Nyssodesmus, Tirodesmus, Nanorrhacus,* and *Rhyphodesmus*) have been recognized at one time or another by American workers. Various others were accepted

by Silvestri in his papers on the neotropical forms and one of these, *Psammodesmus*, becomes the subject of the present paper. The genus is redefined on the basis of gonopod structure and a new species is proposed. The type species designated by Cook has not been examined,[1] but the characters of the genus, as stated in Cook's description, seem to be quite adequate for at least a generic recognition. The specimens at hand keyed out readily to *Psammodesmus* on the basis of nonsexual characters; somewhat later it was found that in gonopod structure they are very close to the two species which Silvestri described in that genus in 1897.

APPLICATION OF THE NAME PLATYRHACUS

The primary difficulty involved in the systematics of the American species is the identity of the type species of *Platyrhacus*. Concerning this matter, Cook wrote (op. cit., p. 51):

> The genus Platyrrhacus was based by C. L. Koch on a Brazilian species, *Polydesmus scaber* Perty, or at least on a specimen so determined, and described as being slightly convex, densely granulate, and with a row of distinct, pearl-like tubercules along the posterior margin of each segment. There are said to be two other rows of somewhat smaller tubercules placed wider apart. Although the carinae are said to be strongly toothed, they appear from the plate that the teeth are broad and rounded. After studying the description in connection with that of another American species described by Koch, *Platyrrhacus rufipes*, the opinion has been gained that it would not be safe to identify it, even generically, with any of the material which has come into my hands for study.

Since no types of Koch's species have ever been found, to my knowledge, and since it was not customary in his time to designate and retain type specimens, it seems to me that some sort of arbitrary action may be needed to resolve the matter satisfactorily. About the only tangible information for a starting point is the likelihood that since Perty's original animal came from Brazil, the specimen identified as *scaber* by Koch most probably had a like provenance even though we can never be sure it was even congeneric with Perty's species.

If *Platyrhacus* as used by Attems is to be divided into more natural genera, the generic name in its restricted sense must be applied to one of the South American genera. Attems disregarded this necessity in designating *Polydesmus pfeifferae* Humbert and Saussure, 1869, an East Indian species, as type of the genus.

There is a considerable number of recognizable American genera, distinguished for the most part by the structure of the gonopods. Of these genera, *Tirodesmus* and *Aymaresmus* are disqualified, so far as application of the name *Platyrhacus* is concerned, because of the shape of the keels in those two groups. Of the remainder, it seems best to apply the name to that genus which is most numerous in species and has the widest range; and thus would be most likely encountered by early collectors. The group which most readily qualifies is that including *clathratus*, *bilineatus*, *propinquus*, *tenebrosus*, and their close relatives. It extends from Nicaragua into western Brazil. There is nothing in Koch's description and plate to preclude association of his generic name with this group (of which Cook apparently had seen no specimens—cf. the last sentence of his paragraph quoted above).

It is felt that an eventual decision regarding the identity of *P. scaber*, involving a redescription and designation of type specimens, will be desirable and necessary for a final settlement of this issue. At the present time this step can not be taken, in the lack of adequate material for study.

Should the present allocation meet with general approval, it will become necessary to select one of the numerous generic names already available for the group of Indonesian species treated by Attems in his subgenus *Platyrhacus*. Ten such names (proposed by Cook, Pocock, and Silvestri) are listed as synonyms in Attems's account. Since his "subgenus" seems clearly to be heterogeneous, it is probably advisable to delay nomenclatorial settlement until at least a partial

[1] *Psammodesmus cos* was based on a specimen lent to Cook by the Academy of Natural Sciences of Philadelphia. Dr. J. A. G. Rehn, curator of insects at that institution, informs me that it is not now in their collection and probably was not returned. I have not been able to locate it in the National Museum collection, wherein most of Cook's material was deposited.

restudy of the East Indian forms has been made.[2]

Genus **Psammodesmus** Cook

Psammodesmus Cook, 1896, Brandtia, no. 12: 52.—Silvestri, 1897, Boll. Mus. Torino **12** (305): 15.
Platyrhacus subgenus *Tirodesmus* Attems, 1938, Das Tierreich, Lief. **69**: 229 (in part).
Ernostyx Chamberlin, 1941, Bull. Amer. Mus. Nat. Hist. **78**: 497 (type, *E. moyobambus* Chamberlin).

Type species.—*Psammodesmus cos* Cook, by original designation.

Generic diagnosis.—Platyrhacid millipeds characterized by the following combination of features: Dorsum slightly arched, keels set high on sides; lateral edges of keels almost smooth, bearing only two or three small teeth (somewhat emarginate in *moyobambus*); tergites divided into three transverse rows of poorly defined polygonal areas, each of which has a tiny median tubercule; repugnatorial pores small, removed from the edge of the keels by a distance of from 2 to 6 times the diameter of the peritreme area; collum with an anterior row of large tubercules, behind which is a distinct transverse depression.

Male gonopods with the prefemur and femur coalesced into a rather stout, straight, and unmodified trunk, terminating distally in a large flattened tibiotarsal blade and a tapering, slender solenomerite branch. The genus is especially characterized by the fact that these terminal elements are bent in a direction *away from* the coxal portion of the gonopod. The impression given is that of an arm bent at a right angle at the elbow, with the thumb and opposed cupped fingers pointing away from the shoulder. In the genus *Platyrhacus* the tibiotarsus and solenomerite are bent in the opposite direction—back toward the coxa.

Synonymy.—Attems (*op. cit.*, p. 226) grouped almost all the American platyrhacids in a subgenus to which he applied Cook's name *Tirodesmus* (type, *fimbriatus* Peters). It is felt that this species is quite worthy of generic distinction from the other Neotropical forms (because of the characteristic shape of the lateral carinae as well as the male gonopods); *Tirodesmus* is at present considered to be monospecific.

Chamberlin has recently described several new genera of the family from northeastern Peru. It is apparent from his paper that he did not consider the known diplopod faunas of immediately adjacent countries such as Ecuador and Brazil; furthermcre the drawings given for his genus *Ernostyx* are strongly suggestive of the sort typical of *Psammodesmus*. At my request, Dr. Willis J. Gertsch very generously lent the holotype of *Ernostyx moyobambus* from the collection of the American Museum of Natural History. Examination of this specimen disclosed that it is congeneric with the new species of *Psammodesmus* to be described (cf. Figs. 4, 5), and that if my understanding of that genus is correct, *Ernostyx* must fall as a junior synonym.

Species.—Eight.

Range.—Cordilleran region of northwestern South America; from northeastern Peru to the isthmus of Panama.

Psammodesmus schmitti Loomis and Hoffman, n. sp.[3]

Figs. 1–4

Type specimens.—Male holotype in the collection of the U. S. National Museum; collected at Port Obaldia, Province of Darién, Panama, by H. Pittier (around 1914). Two male paratypes, also in the National Museum, from Cana, Province of Darién, collected by E. A. Goldman in June 1912.

Diagnosis.—Characterized primarily by the shape of the tibiotarsal lamina of the male gonopod. Its distal edge is gently arcuate, only slightly extended beyond the level of the solenomerite. In the other known species the distal

[2] Attems's treatment of the Platyrhacidae leaves much to be desired in the way of consistency. Despite his inclination to reduce the number of supraspecific categories as much as possible, his own groupings are not always defensible. A case in point is the subgenus *Ozorhacus*, proposed in Das Tierreich (**69**: 253) for the inclusion of 10 species. As shown by the illustrations of the gonopods, none of the referred forms are closely related to the type species (*katantes* Attems). Rather, of them, *amblyodon* and *coelebs* are very close to *singulus* and *microporus*, respectively, which Attems places in the subgenus *Platyrhacus*; *mortoni*, *postumus*, *tetanotropis*, and *sarasinorum* are allied with the group of species (particularly *mediotaeniatus*) placed by Attems in *Psaphodesmus*. Furthermore, *fecundus* and *sterilis* on the one hand, and *arietis* on the other, cannot be allocated to any currently recognized grouping; doubtless generic names will have to be proposed for them.

[3] This species was recognized as new and a description was prepared by H. F. Loomis from the Port Obaldia specimen. On learning of my interest in *Psammodesmus* he kindly forwarded the specimen and his description and drawings. All these have been utilized in the above text, and it seems appropriate to consider the species as described jointly by Loomis and myself.

margin of this part is produced upwards into a pronounced angulation.

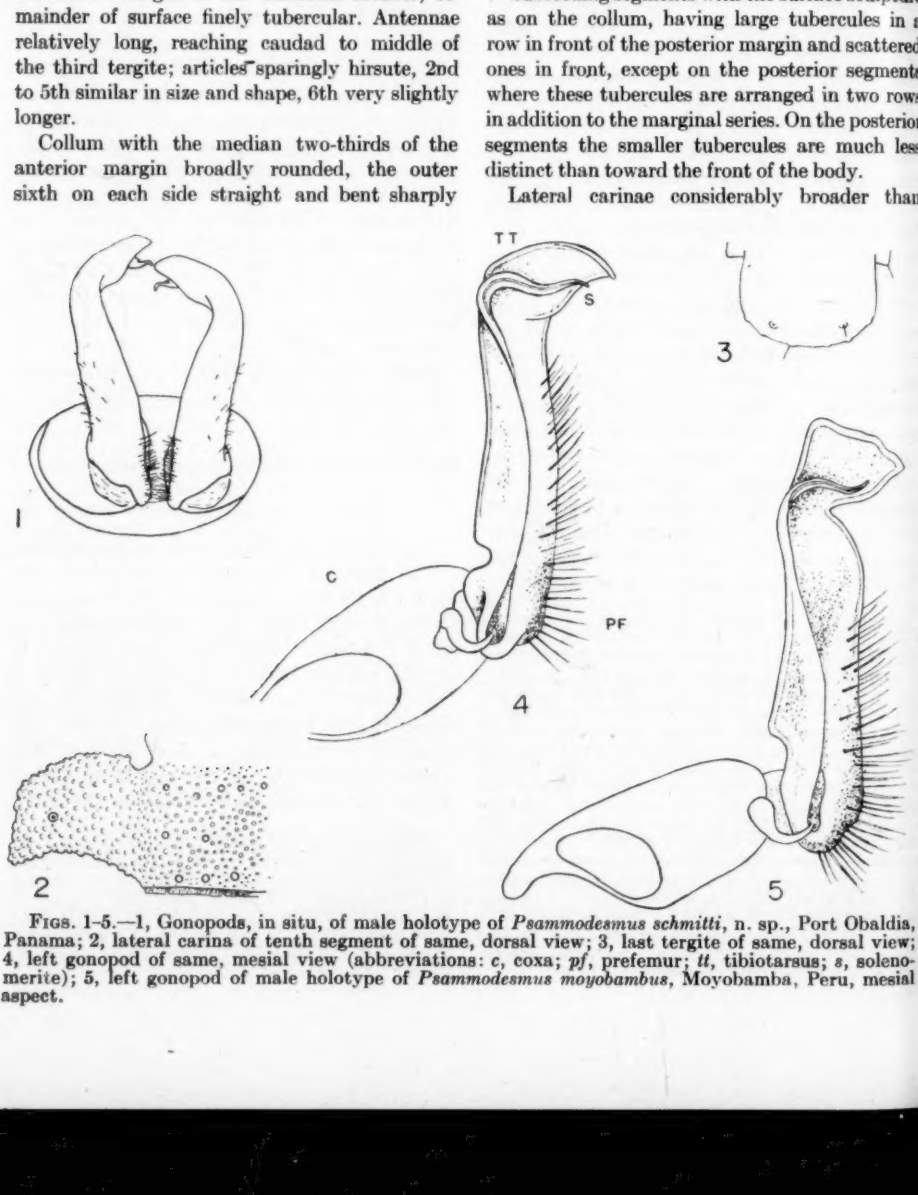
Description of type.—Body 53 mm long and 9.5 mm wide. Dorsum moderately convex; lateral carinae projecting from above the middle of the body, slightly deflexed and extending far from the sides, decidedly broader than long, anterior margin with a prominent square shoulder at the base.

Head with the ridges of the vertex broad, tortuous, converging backward but not quite meeting at the groove; shining-coriaceous clypeal area triangular with the upper angle opposite the lower margin of the antennal sockets; remainder of surface finely tubercular. Antennae relatively long, reaching caudad to middle of the third tergite; articles sparingly hirsute, 2nd to 5th similar in size and shape, 6th very slightly longer.

Collum with the median two-thirds of the anterior margin broadly rounded, the outer sixth on each side straight and bent sharply ectocaudad and with 6 to 8 rounded crenations or nodules; outer fourth of the posterior margin on each side slanting obliquely inward to the transverse median half. Surface of the segment densely beset with small tubercules and a row of 10 to 12 large, rounded, pearllike ones just behind the median portion of the front margin; another row of 8 to 10 similar tubercules near the posterior margin, and the disk with 8 to 10 large scattered tubercules. Behind the depression following the anterior row of tubercules the surface of the segment is raised into a reniform swelling, having the emargination in front.

Succeeding segments with the surface sculpture as on the collum, having large tubercules in a row in front of the posterior margin and scattered ones in front, except on the posterior segments where these tubercules are arranged in two rows in addition to the marginal series. On the posterior segments the smaller tubercules are much less distinct than toward the front of the body.

Lateral carinae considerably broader than



FIGS. 1–5.—1, Gonopods, in situ, of male holotype of *Psammodesmus schmitti*, n. sp., Port Obaldia, Panama; 2, lateral carina of tenth segment of same, dorsal view; 3, last tergite of same, dorsal view; 4, left gonopod of same, mesial view (abbreviations: *c*, coxa; *pf*, prefemur; *tt*, tibiotarsus; *s*, solenomerite); 5, left gonopod of male holotype of *Psammodesmus moyobambus*, Moyobamba, Peru, mesial aspect.

long, with a distinct shoulder in front just ectad of the base; posterior angles very gradually increasing in length toward the back. Nineteenth segment with the keels bent caudad and their posterior margins almost longitudinal. Pore formula normal; the pores surrounded by a broad, flat rim (peritreme); pores remote from the margins of the keels—being 4 to 7 times the diameter of the pore area from the outer margin, and 3 to 4 times its diameter from the posterior margin. In the drawing of the carina of segment 10 (Fig. 2) the pore appears about equidistant from the outer and posterior margins. However the downward slant of the carina causes a foreshortening effect and the pore is actually much more remote from the outer than from the posterior margin.

Last segment elongate-rounded; below and at the base of this dorsal production the surface on each side is produced into a distinct setiferous tubercule (Fig. 3).

Anal valves with each raised margin bearing a setiferous tubercule above, and another tubercule on the disk of each valve close to the margin below the middle.

Preanal scale with the anterior production covering a considerable portion of the ventral posterior margin of the last segment; setiferous tubercules of the posterior margin long, closely placed, divergent, the margin between them short, rounded-acute.

Ventral surfaces and legs generally very smooth and shining. Prozonites somewhat longer than metazonites. Legs attached to a small raised area that is noticeably elevated above the level of the prozonite. Spiracles opening through small rounded tubercules, one above the insertion of each leg.

Legs moderately long (apical third of third joint visible from above when legs are extended) and slender, sparingly bristled. Length of joints, in decreasing order of length, 3-6-5-2-4-1. Third joint slightly longer than the basal two. Anterior legs without processes. Tubercules of the sterna between legs 4, 5, and 6 distinctly compressed from side to side, other sterna with rounded tubercules at the bases of the legs.

Gonopods projecting from a rounded-ovate sternal aperture, the posterior margin of which is strongly elevated. Seen in ventral aspect, the gonopods (Fig. 1) appear nearly straight for two-thirds of their length, with the distal third bent at a 45 degree angle mesiad and away from the sternites. Coxae of gonopods rather small, somewhat ovoid, without projections or large hairs. Prefemur and femur inseparable, unless the point of their coalescence is indicated by an indentation on the side near the coxa (this indentation is also present in *moyobambus*). Setose area along outer margin extends about two-thirds the length of the joint, which is robust and relatively straight. Course of seminal channel indicated by a long gently arcuate groove. Tibiotarsus represented by a large, somewhat crescent-shaped blade, the terminal end of which points away from the coxa. The distal margin of this part is arcuate, the free proximal margin concave, as shown in the drawing. Arising at the base of the tibiotarsus is a slender, unbranched, somewhat sinuate solenomerite.

After 40 years of preservation the specimen is completely bleached, and no conjecture can be made concerning the color of the living animal.

Remarks.—The two paratypes from Cana differ slightly in that sternal spines are so faint as to be easily overlooked. In them, too, the tergites show a tendency to be divided into three transverse rows of polygonal areas which are, however, perceptible only with the specimens dried. The gonopods of all three specimens are identical in every respect.

The species is named for Dr. Waldo L. Schmitt, head curator of zoology in the U. S. National Museum, in recognition of his contributions to the knowledge of Middle American Crustacea and in appreciation of his cooperation and assistance which have greatly facilitated my work at the U. S. National Museum.

THE SPECIES OF PSAMMODESMUS

Eight species are at present referable to the genus. It is a matter of some regret that males of the type species are as yet unknown; however, it is believed that *P. cos* can readily be distinguished on the basis of nonsexual characters. Another species is likewise known only from the female sex. This was described by Chamberlin (op. cit) as *Platyrrhacus cainarachus*. The description and figures given, however, agreed so well with the characters of *Psammodesmus* that the type specimen of *cainarachus* was reexamined. I am again indebted to Dr. Gertsch for making this specimen available for examination. It is clearly a species of

Psammodesmus, and very close to *moyobambus*.

In order to summarize what is now known about the genus, I subjoin a tentative key for identification of the species, and a list indicating pertinent literature and distribution.

1. Repugnatorial pores removed from edge of keel by a distance of 5 or 6 times the diameter of the peritreme.....*cos* Cook
   Repugnatorial pores removed from edge of keel by a distance generally not exceeding 4 times diameter of the peritreme.....2
2. Lateral margin of midbody keels excavated or indented adjacent to the pores.....3
   Lateral margins of keels not excavated or indented.....4
3. Dorsal tubercules of normal, moderate size, at most hemispherical in shape
   moyobambus (Chamberlin)
   Dorsal tubercules enlarged, higher than wide and very prominent
   cainarachus (Chamberlin)
4. Solenomerite short, simply arcuate
   chuncho (Chamberlin)
   Solenomerite longer, definitely bisinuate or somewhat sigmoid in shape.....5
5. Tibiotarsus of gonopod semicircular or nearly so in shape, its inner edge straight and indented from inner edge of femur, thus exposing base of solenomerite.....6
   Tibiotarsus not semicircular, its inner (or distal) margin continuous with that of femur, not exposing base of the solenomerite.....7
6. Dorsum dark brown, with the keels lighter
   cameranii Silvestri
   Dorsum dark gray with two paramedian longitudinal light gray stripes
   fasciolatus Silvestri
7. Tibiotarsus subcrescentic in shape
   schmitti Loomis and Hoffman
   Tibiotarsus subtriangular in shape
   dasys (Chamberlin)

PSAMMODESMUS

cos Cook:
Brandtia, no. 12: 52. 1896.
Colombia.

cameranii Silvestri:
Boll. Zool. Mus. Torino **12** (305): 15, fig. 41. 1897.
Ecuador: San José, Gualaquiza, San Antonio.

fasciolatus Silvestri:
Boll. Zool. Mus. Torino **13** (324): 4, fig. 6. 1898.
Ecuador: Río Peripa.

cainarachus (Chamberlin):
Bull. Amer. Mus. Nat. Hist. **78** (7): 491, figs. 116, 117, 1941.
Peru: Dept. of Loreto, Río Cainarachi.

chuncho (Chamberlin):
Bull. Amer. Mus. Nat. Hist. **78** (7): 497, fig. 197A. 1941.
Peru: Dept. of Loreto, Iquitos.

dasys (Chamberlin):
Bull. Amer. Mus. Nat. Hist., **78** (7): 497, figs. 193–96. 1941.
Peru: Dept. of Loreto, Contayo Hills, Río Tapiche.

moyobambus (Chamberlin):
Bull. Amer. Mus. Nat. Hist. **78** (7): 498, figs. 188–92. 1941.
Peru: Dept. of Loreto, Moyobamba, Balsapuerto Trail.

schmitti Loomis and Hoffman
Journ. Washington Acad. Sci. **43**: 301–303, figs. 1–4. 1953.
Panama: Prov. of Darién; Cana, Port Obaldia.

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